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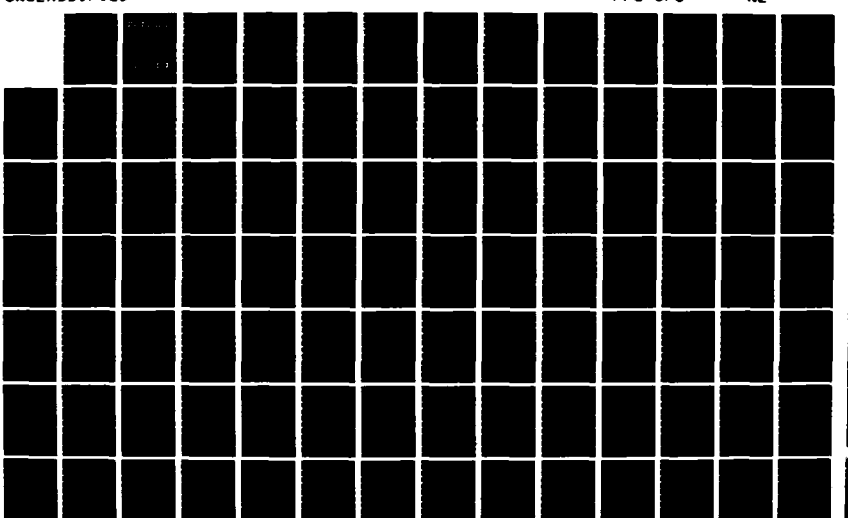

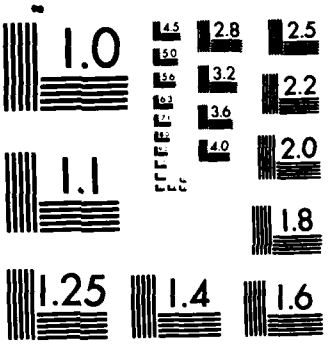

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EARLY LIMNOLOGY OF DWORSHAK RESERVOIR

AD-A163 043

PART 1 – LIMNOLOGY

PART 2 – IMPACT OF LOG LEACHATES ON PHYTOPLANKTON

PART 3 – FATE OF PHYTOPLANKTON AND ZOOPLANKTON DYNAMICS

PART 4 – BACTERIOLOGY

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Dworshak Reservoir, Idaho
Limnology

20. ABSTRACT *(Continue on reverse side if necessary and identify by block number)*

The limnology of Dworshak Reservoir, a very deep, cold water reservoir on the North Fork of the Clearwater River in North Idaho was studied in the first three years after filling. The 53-mile long lake is monomictic in the lower 10 miles, and dimictic in the middle and upper reaches. Mean temperature of the pool decreased from a 1972 high of 51.2 F, to 49.7 F in 1973 and 46.0 F in 1974. Surface waters did attain 80 F in August, 1973, but thermocline depths were shallow (20-35 feet throughout the summer) providing for mean deep water temperatures of less than 43 F. Temperatures at 600 feet remained at 40 F (± 1F

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year round.

The submergence of soils and vegetation in conjunction with an Anabaena bloom in July, 1972, resulted in high bacterial counts, increased algal nutrient concentrations over inflow concentrations, the initiation of zooplankton cycling, and anaerobic conditions below 550 feet until late 1973. Deep O_2 concentrations have increased since mid 1973. Total dissolved solids as indicated by conductivity, have shown no overall decline from 1972 to 1974 (28 to 19 μmhos). Mean nitrate and orthophosphate concentrations have remained at approximately .05 and .018 mg l^{-1} respectively, but intense short term fluctuations of nitrate and orthophosphate have periodically taken these nutrients to detection limits. Average phytoplankton cell numbers have sharply dropped at all stations from 3×10^6 cells l^{-1} in 1972 to approximately 0.4×10^6 cells l^{-1} in 1974. High turbidity in 1974 from shoreline wave erosion and slumping reduced 1974 algal production to levels below projections based upon available nutrients. Carbon-14 uptake showed similar patterns. After 3 years, Dworshak Reservoir dropped from a moderately productive to an oligotrophic body of water.

The major objective of this limnological program was to describe the water quality and plankton ecology of Dworshak Reservoir. Supplemental objectives were: 1) To evaluate the impact of standing timber left below minimum pool in the reservoir on water quality and plankton; 2) to evaluate the impact of reservoir operations on water quality and plankton; 3) to describe apparent interdependencies within the plankton community; and, 4) to provide a description of the temporal and spatial distribution of plankton communities, a principle food base of the reservoir fishery.

EARLY LIMNOLOGY OF DWORSHAK RESERVOIR

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Final Report Submitted to

U.S. Army Corps of Engineers
Walla Walla District
Walla Walla, Washington 99362

Contract No. DACW68-72-C-0142

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LIMNOLOGY

Part 1 of

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TABLE OF CONTENTS

Page

LIST OF FIGURES 1-iv

LIST OF TABLES 1-vii

ABSTRACT 1-x

INTRODUCTION 1-1

Supplemental objectives 1-1

METHODOLOGY 1-5

Primary Production 1-6
Zooplankton 1-6
Sampling and Counting 1-6

RESULTS AND DISCUSSION 1-11

Thermal Patterns 1-11
Water Transparency 1-27
Dissolved Oxygen 1-44
Hydrogen Sulfide 1-55
Water Chemistry 1-55
Phytoplankton 1-64
Zooplankton 1-74
Regression Analyses 1-88

CONCLUSIONS 1-106

RECOMMENDATIONS 1-108

LITERATURE CITED 1-110

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LIST OF FIGURES

Figure		Page
1.	Dworshak Reservoir with stations of the 1972-1974 study. .	1-2
2.	Temperature patterns (F) at RM 3 in Dworshak Reservoir, 1972-1974.	1-16
3.	Temperature patterns (F) at RM 19 in Dworshak Reservoir, 1972-1974.	1-17
4.	Temperature patterns (F) at RM 35 in Dworshak Reservoir, 1972-1974.	1-18
5.	Temperature patterns (F) at EC 4 in Dworshak Reservoir, 1972-1974.	1-19
6.	Temperature patterns (F) at LNFK 1 in Dworshak Reservoir, 1972-1974.	1-20
7.	Longitudinal temperature profiles (F) in Dworshak Reservoir, 1972.	1-21
8.	Longitudinal temperature profiles (F) in Dworshak Reservoir, 1973.	1-22
9.	Longitudinal temperature profiles (F) in Dworshak Reservoir, 1974.	1-23
10.	Depth of metalimnion midpoint in Dworshak Reservoir at RM 3, 1972-1974.	1-24
11.	Comparison of Dworshak Reservoir mean monthly inflow vs. outflow temperatures 1972-1974	1-28
12.	Turbidity (FTU) at RM 3 in Dworshak Reservoir, 1972-1974 .	1-30
13.	Turbidity (FTU) at RM 19 in Dworshak Reservoir, 1972-1974.	1-31
14.	Turbidity (FTU) at RM 35 in Dworshak Reservoir, 1972-1974.	1-32
15.	Turbidity (FTU) at EC 4 in Dworshak Reservoir, 1972-1974 .	1-33
16.	Turbidity (FTU) at LNFK 1 in Dworshak Reservoir, 1972-1974	1-34
17.	Annual minimum and maximum secchi disc transparency at 5 stations in Dworshak Reservoir, 1972-1974.	1-38
18.	Average subsurface light penetration in the spring and summer-fall at RM 3 in Dworshak Reservoir, 1972-1974 . . .	1-39

LIST OF FIGURES (Continued)

Figure		Page
19.	Average subsurface light penetration in the spring and summer-fall at RM 19 in Dworshak Reservoir, 1972-1974. . .	1-40
20.	Average subsurface light penetration in the spring and summer-fall at RM 35 in Dworshak Reservoir, 1972-1974. . .	1-41
21.	Average subsurface light penetration in the spring and summer-fall at EC 4 in Dworshak Reservoir, 1972-1974 . . .	1-42
22.	Average subsurface light penetration in the spring and summer-fall at LNFK 1 in Dworshak Reservoir, 1972-1974 . .	1-43
23.	Dissolved oxygen (mg/1) at RM 3 in Dworshak Reservoir, 1972-1974.	1-45
24.	Dissolved oxygen (mg/1) at RM 19 in Dworshak Reservoir, 1972-1974.	1-46
25.	Dissolved oxygen (mg/1) at RM 35 in Dworshak Reservoir, 1972-1974.	1-47
26.	Dissolved oxygen (mg/1) at EC 4 in Dworshak Reservoir, 1972-1974.	1-48
27.	Dissolved oxygen (mg/1) at LNFK 1 in Dworshak Reservoir, 1972-1974.	1-49
28.	Longitudinal oxygen profiles (mg/1) in Dworshak Reservoir, 1972	1-50
29.	Longitudinal oxygen profiles (mg/1) in Dworshak Reservoir, 1973	1-51
30.	Longitudinal oxygen profiles (mg/1) in Dworshak Reservoir, 1974	1-52
31.	Conductivity (µmhos/cm) at RM 3 in the 0-40 foot layer of Dworshak Reservoir, 1972-1974	1-57
32.	NO_3 and 0-PO_4 concentration (mg/1) in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-1974	1-63
33.	Mean total phytoplankton in the 0-40 foot layer at RM 19 in Dworshak Reservoir, 1972-1974	1-67
34.	Mean total phytoplankton in the 0-40 foot layer at RM 35 in Dworshak Reservoir, 1972-1974	1-68

LIST OF FIGURES (Continued)

Figure — Page

35. Mean total phytoplankton in the 0-40 foot layer at RM 19 in Dworshak Reservoir, 1972-1974 1-69

36. Mean total phytoplankton in the 0-40 foot layer at EC 4 in Dworshak Reservoir, 1972-1974 1-70

37. Mean total phytoplankton in the 0-40 foot layer at LNFK 1 in Dworshak Reservoir, 1972-1974 1-71

38. Average summer-fall (June-October) algae numbers in the 0-40 foot layer of Dworshak Reservoir, 1972-1974 1-77

39. Mean carbon uptake in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-1974. 1-78

40. Mean carbon uptake in the 0-40 foot layer at EC 4 in Dworshak Reservoir, 1972-1974. 1-79

41. Mean total zooplankton in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-1974. 1-80

42. Mean total zooplankton in the 0-40 foot layer at RM 19 in Dworshak Reservoir, 1972-1974. 1-81

43. Mean total zooplankton in the 0-40 foot layer at RM 35 in Dworshak Reservoir, 1972-1974. 1-82

44. Mean total zooplankton in the 0-40 foot layer at EC 4 in Dworshak Reservoir, 1972-1974. 1-83

45. Mean total zooplankton in the 0-40 foot layer at LNFK 1 in Dworshak Reservoir, 1972-1974 1-84

46. Mean summer-fall (June-October) zooplankton composition in the 0-40 foot layer of Dworshak Reservoir, 1972-1974. . 1-85

47. Zooplankton egg and adult counts in the 0-40 foot stratum of Dworshak Reservoir at RM 3, 1974. 1-87

LIST OF TABLES

Table		Page
1.	General specifications of Dworshak Dam and Reservoir, North Fork of the Clearwater River, Idaho	I-4
2.	Period list 1972 through 1974 and station designation	I-8
3.	Flow sheet for laboratory chemical analyses of Dworshak Reservoir water samples, 1972-1974.	I-10
4.	Volume (acre feet x 10^3) of depth strata in Dworshak Reservoir as a function of surface elevation.	I-12
5.	Means and ranges of selected limnological parameters in Dworshak Reservoir 1972-1975. All stations and all depths averaged.	I-14
6.	Means and ranges of selected chemical parameters, light intensity, and algal production in Dworshak Reservoir, 1972-1974. All stations and all depths averaged.	I-15
7.	Mean temperature per unit volume of water in Dworshak Reservoir at time of maximum heat content (August).	I-26
8.	Minimum and maximum secchi disc in Dworshak Reservoir, 1972-1974	I-37
9.	Mean vertical extinction coefficients in Dworshak Reservoir, 1972-1974.	I-37
10.	Mean oxygen percent saturation of surface (S-40 feet) and deep (below 100 foot) layers of Dworshak Reservoir, 1972-1974.	I-54
11.	Summer hypolimnial oxygen deficits in Dworshak Reservoir, 1972-1974 (from onset of stratification to maximum stratification.	I-54
12.	Mean nitrate and ortho-phosphate concentrations (mg/l) in the 0-40 foot layer of Dworshak Reservoir, 1972-1974.	I-59
13.	Trace metals concentrations (mg/l) at RM 3 in Dworshak Reservoir, 1972-1974.	I-60
14.	Overall means of phytoplankton cell numbers per liter in the 0-40 foot stratum of Dworshak Reservoir, 1972-1974.	I-65
15.	Predominant phytoplankton genera comprising peaks in 1972-1974 at RM 3 in Dworshak Reservoir.	I-66

LIST OF TABLES (Continued)

Table Page

16. Summer-fall average bluegreen algae (cells/1) in Dworshak Reservoir 0-40 foot layer, 1972-1974 1-73

17. Overall means of zooplankton numbers per cubic meter in the 0-33 foot stratum of Dworshak Reservoir, 1972-1974 . . 1-75

18. Predominant zooplankton genera comprising peaks at RM 3 in Dworshak Reservoir, 1972-1974 1-76

19. Simple correlation coefficients between selected limnological variables at RM 3 in Dworshak Reservoir, 1972-1974 1-90

20. Simple correlation coefficients between selected limnological variables at RM 19 in Dworshak Reservoir, 1972-1974 1-91

21. Simple correlation coefficients between selected limnological variables at RM 35 in Dworshak Reservoir, 1972-1974 1-92

22. Simple correlation coefficients between selected limnological variables at EC 4 in Dworshak Reservoir, 1972-1974 1-93

23. Simple correlation coefficients between selected limnological variables at LNFK 1 in Dworshak Reservoir, 1972-1974 1-94

24. The relationship of percent oxygen saturation to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-95

25. The relationship of ortho phosphate and carbon to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS). 1-96

26. The relationship of ortho phosphate and bicarbonate to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS). 1-97

27. The relationship of total algae to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-98

28. The relationship of diatoms to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-99

LIST OF TABLES (Continued)

Table — Page

29. The relationship of green algae to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-100

30. The relationship of bluegreens to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-101

31. The relationship of algal productivity to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-102

32. The relationship of total bacteria to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS). 1-103

33. The relationship of coliform bacteria to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-104

34. The relationship of zooplankton to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS) 1-105

ABSTRACT

The limnology of Dworshak Reservoir, a very deep, cold water reservoir on the North Fork of the Clearwater River in North Idaho was studied in the first three years after filling. The 53-mile long lake is monomictic in the lower 10 miles, and dimictic in the middle and upper reaches. Mean temperature of the pool decreased from a 1972 high of 51.2 F, to 49.7 F in 1973 and 46.0 F in 1974. Surface waters did attain 80 F in August, 1973, but thermocline depths were shallow (20-35 feet throughout the summer) providing for mean deep water temperatures of less than 43 F. Temperatures at 600 feet remained at 40 F ($\pm$ 1 F) year round.

The submergence of soils and vegetation in conjunction with an Anabaena bloom in July, 1972, resulted in high bacterial counts, increased algal nutrient concentrations over inflow concentrations, the initiation of zooplankton cycling, and anaerobic conditions below 550 feet until late 1973. Deep O_2 concentrations have increased since mid 1973. Total dissolved solids as indicated by conductivity, have shown no overall decline from 1972 to 1974 (28 to 19 µmhos). Mean nitrate and orthophosphate concentrations have remained at approximately .05 and .018 mg l^{-1} respectively, but intense short term fluctuations of nitrate and orthophosphate have periodically taken these nutrients to detection limits. Average phytoplankton cell numbers have sharply dropped at all stations from 3 x 10^6 cells l^{-1} in 1972 to approximately 0.4 x 10^6 cells l^{-1} in 1974. High turbidity in 1974 from shoreline wave erosion and slumping reduced 1974 algal production to levels below pro-

jections based upon available nutrients. Carbon-14 uptake showed similar patterns. Declining reservoir productivity is illustrated by overall reservoir means of total zooplankton numbers: 2.73 x $10^4/m^3$ in 1972, 1.85 x $10^4/m^3$ in 1973, and 1.08 x $10^4/m^3$ in 1974. After 3 years, Dworshak Reservoir dropped from a moderately productive to an oligotrophic body of water.

INTRODUCTION

Impoundment of the North Fork of the Clearwater River in north Idaho created a greatly changed, new type of aquatic environment. Post-impoundment conditions both within the storage reservoir and downstream in the main Clearwater River differ profoundly from those in the free-flowing river. In anticipation of these changes, the U.S. Army Corps of Engineers contracted a three year reservoir limnological study to the University of Idaho in March, 1972 (Contract DACW68-72-C-0142). The program was later ammended by a contract change order of July 31, 1973.

The major objective of this limnological program was to describe the water quality and plankton ecology of Dworshak Reservoir, a 53 mile long cold, deep-water storage reservoir on the North Fork of the Clearwater River (Figure 1).

Supplemental objectives were:

1) To evaluate the impact of standing timber left below minimum pool in the reservoir on water quality and plankton;
2) To evaluate the impact of reservoir operations on water quality and plankton;
3) To describe apparent interdependencies within the plankton community; and,
4) To provide a description of the temporal and spatial distribution of plankton communities, a principle food base of the reservoir fishery.

Physical aspects of the dam are described in Design Memorandum I of October, 1960. The reservoir limnology research program was first

	RM-3	RM-19	RM-35	EC-4	LNFK-1
Maximum Depth	625'	445'	290'	410'	195'
Minimum Depth	470'	290'	135'	255'	40'
Channel Width	3,505'	1,398'	1,383'	1,066'	1,036'

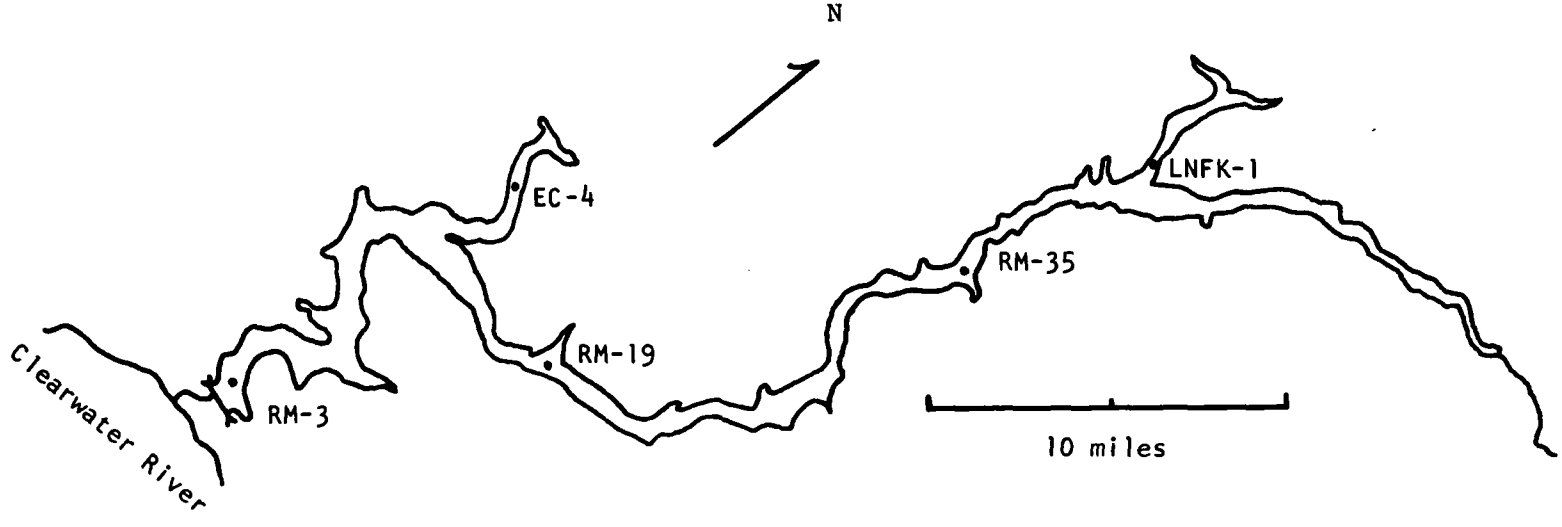


Figure 1. Dworshak Reservoir with stations of the 1972-1974 study.

described in the Technical Studies Work Plan on Dworshak Reservoir (May 14, 1971).

Physical specifications of Dworshak dam, reservoir, and the North Fork of the Clearwater River are presented in Table 1. Dworshak Reservoir began filling in September, 1971 and attained full pool by spring, 1973.

The North Fork of the Clearwater River drains a mountainous and forested watershed of 2440 square miles. The river flows through Columbia River basalt and exposed metamorphosed sediments with granitic intrusions. The principle rocks exposed in the reservoir area include granitic gneiss, granite, and basalt. Clay content in the soils is low to medium with medium to high silt content. Surface soils in the area of the reservoir are relatively shallow (20-50 in). The topography in the area is steep with slopes commonly between 40 and 70 percent.

The North Fork of the Clearwater River reaches a peak flow in mid May of approximately 15-20 thousand cubic feet per second (cfs). Average annual flow is 4-8 thousand cfs. Two major tributaries to the reservoir are the Little North Fork of the Clearwater River and Elk Creek.

Climate in the reservoir area is characterized by mild summers and long, cold winters with considerable snowfall. The annual precipitation near the dam averages 24 in. and increases toward upper reaches of the reservoir. The mean annual temperature at Orofino, Idaho, is 10 C with recorded extremes of 48 C and -31 C (U.S. Army Corps of Engineers, 1969).

Table 1. General specifications of Dworshak Dam and Reservoir, North Fork of the Clearwater River, Idaho

DAM	River Mile 1.9	
	Straight axis concrete gravity	
	Overflow spillway with two tainter gates	
	Three turbines with 400,000 KW total capacity	
RIVER	Mean annual streamflow	5,727 cfs.
	Minimum of record	250 cfs.
	Maximum of record	100,000 cfs.
	Mean annual streamflow	4.1×10^6 A ft.
RESERVOIR	Surface area	17,090 Acres
	Maximum water depth	635 ft.
	Minimum surface elevation	1445 ft.
	Storage capacity (gross)	3.468×10^6 A ft.
	Storage capacity (usable)	2.016×10^6 A ft.
	Maximum surface elevation	1600 ft.
	Reservoir length	53.6 mi.
	Shoreline length	175 mi.
	Mean water retention time	10.2 months

METHODOLOGY

This report presents findings of limnological sampling from April 1972 through November 1974. Reservoir sampling was conducted by limnology teams from the Walla Walla District, Corps of Engineers in conjunction with the University of Idaho College of Forestry and Department of Bacteriology. The following parameters were measured:

Temperature - Thermistor probe and/or Bathythermograph

Light penetration - Montedoro/Whitney Underwater Photometer and Secchi disc

Oxygen - Winkler (Azide modification)

pH - Sargent Welch pH meter

Turbidity - Hach 2100 Turbidimeter

Total dissolved solids - Lab Line Electro-mhometer

Alkalinity
Carbon dioxide
Dissolved organic matter
Nitrates
Phosphates
Iron
Biochemical oxygen demand
Silicates
Hydrogen sulfide

} Standard Methods (1971) (Table 3)

Algae composition, numbers, chlorophyll, and biomass

Primary production

Zooplankton composition, numbers, and biomass

Total, coliform, and fecal coliform bacteria

Algal growth response

Zooplankton grazing

Log leachate assays

Algal samples were preserved with Lugol's solution, then identified, counted, and measured with a Wild inverted microscope. Detailed explanation of the methodologies of the zooplankton grazing and log leachate experimental work follows in Parts 2 and 3.

Primary Productivity

Primary productivity was estimated at each station during 1973 and 1974 by the ^{14}C light- and dark-bottle method (Slack et al., 1973). Productivity was estimated at surface, 10 ft, and 20 ft depths from 4 hour midday incubations which coincided with phytoplankton sampling.

ZOOPLANKTON

Sampling and Counting

Zooplankton was sampled on the same dates as phytoplankton. A number 10 mesh net on a Miller sampler was towed to filter 1500-2000 l of water. Tows were made at 3 ft and 33 ft depths in 1973. One hundred ft to surface oblique tows were added in 1974. Samples were preserved in 10 percent formalin for later counting of 5-10 ml subsamples at 30X magnification.

Total Daphnia schodleri and Bosmina longirostris eggs were counted in all samples from the main reservoir station in 1974 for calculation of birth rates.

Dworshak Reservoir study sites and their designations as used in this report are as follows (also see Figure 1).

Location	Maximum Depth	Designation
North Fork of the Clearwater River Mile 3	635 ft.	RM 3
Elk Creek River Mile 4	315 ft.	EC 4
North Fork of the Clearwater River Mile 19	441 ft.	RM 19
North Fork of the Clearwater River Mile 35	287 ft.	RM 35
Little North Fork of the Clearwater River Mile 1	175 ft.	LNFK 1

All sites were sampled at least monthly April through November in 1972. Throughout 1973, we sampled more intensely at EC 4 (twice monthly July through November) and RM 3 (weekly July through August) but only twice monthly September through November. Biological activity is maximal when surface water temperatures exceed 10 C; sampling was therefore concentrated in spring, summer, and fall months and in epilimnial waters. This schedule was maintained in 1974 but with twice weekly sampling at RM 3 throughout the summer months. Since sampling all stations on the same day was impossible, the 2 to 4 day interval in which all stations were sampled once is referred to as a "sampling period" (Table 2).

Table 2. Period List 1972 through 1974 and station designation: Each period is the inclusive dates of reservoir sampling.

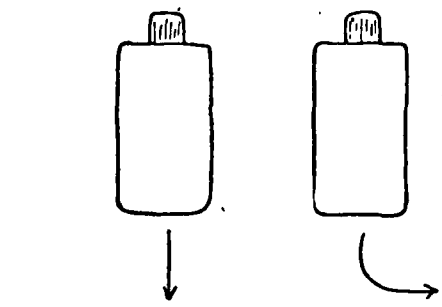
Station Location		Designation
North Fork of the Clearwater River Mile 3	(RM 3)	1
North Fork of the Clearwater River Mile 19	(RM 19)	2
North Fork of the Clearwater River Mile 35	(RM 35)	3
Elk Creek River Mile 4	(EC 4)	4
Little North Fork of the Clearwater River Mile 1	(LNFK 1)	5

YEAR	MONTH	DAYS	PERIOD
1972	May	4-5	7201
	May	16	7202
	May-June	31-2	7203
	June	3	7204
	June	19-20	7205
	July	5-10	7206
	July	19	7207
	August	1-3	7208
	August	15	7209
	September	5-9	7210
	September	21	7211
	October	3-6	7212
	November	2	7213
	November & December	30-3	7214
1973	January	16-17	7301
	March	7-12	7302
	April	4-7	7303
	April	22	7304
	May	3-7	7305
	May	10	7306
	May	18-19	7307
	May	24	7308
	May	31	7309
	June	5-8	7310
	June	14	7311
	June	21-28	7312
	July	4-5	7313
	July	12-15	7314
	July	19	7315
	July	26-27	7316
	August	2	7317
	August	7-9	7318

Table 2. Period List 1972-1975 and station designation (cont'd).

YEAR	MONTH	DAYS	PERIOD
1973	October	12-18	7325
	October	27-28	7326
	November	14-18	7327
	December	1-3	7228
	December	19-28	7229
1974	March	3-9	7401
	March	10-16	7402
	April	1-6	7403
	May	5-11	7404
	May	12-18	7405
	May	19-25	7406
	May-June	26-1	7407
	June	2-8	7408
	June	9-15	7409
	June	16-22	7410
	June	23-29	7411
	June-July	30-6	7412
	July	7-13	7413
	July	14-20	7414
	July	21-27	7415
	July-August	28-3	7416
	August	4-10	7417
	August	11-17	7418
	August	18-24	7419
	August	25-31	7420
	September	1-7	7421
	September	8-14	7422
	September	15-21	7423
	September	22-28	7424
	September-October	29-5	7425
	October	6-12	7426
	October	13-19	7427
	October	20-26	7428
	October-November	27-2	7429
	November	3-9	7430
	November	10-16	7431
	November	17-23	7432
	November	24-30	7433
1975	March	11-13	7501

Table 3. Flow sheet from laboratory chemical analyses of Dworshak Reservoir water samples, 1972-1974.



Two (1) liter samples taken in polyethylene containers (washed according to EPA standards) from each depth at each station. Forty mg/l $HgCl_2$ added as a preservative.

Samples cooled in ice, then frozen on return to University of Idaho.

Back-up samples

Thawed for Analyses

Unfiltered ← → Filtration through 0.45μ Millipore

Test	Total Phosphate	Ortho phosphate - P	Nitrate - N	Sulfate	Silicate
Sample Volume	150 ml.	100 ml.	20 ml.	200 ml.	100 ml.
Method	Persulfate digestion method Std. pg. 526 (13th ed.)	Stannous chloride method Std. pg. 530 (13th ed.)	Brucine method Std. pg. 461 (13th ed.)	Turbimetric method Std. pg. 334 (13th ed.)	Molybdosilicate method Std. pg. 303 (13th ed.)
Technique	Measures all of Ortho PO_4, condensed PO_4 and organically bound PO_4. Except samples are unfiltered and first run through a digestion procedure. (Treatment of samples with a Potassium Persulfate solution and then heating for 30 min. at 15-20 Psi). Samples cooled, neutralized with Sodium Hydroxide, then run through Ortho-PO_4 Test.	Method sensitive for conc. below 0.1 mg P/l. Measures only dissolved Ortho phosphates. Method involves formation of Molybdo Phosphoric Acid, which is reduced to the intensely colored complex Molyhdenus Blue, by Stannous Chloride.	This method recommended for range of .1-2 mg NO_3-N/l. Reaction between Nitrate and Brucine produces a yellow color which can be used for the colorimetric estimation of Nitrate. Heat control significant in this test.	This method best for conc. of SO_4 under 10 mg/l. SO_4 ion is precipitated in a HCl medium with Barium chloride to form Barium sulfate crystals of uniform size. Absorbency of this crystal suspension measured by Spec. 70.	This method is recommended for relatively pure waters containing from 0.4 to 25 mg/l silica. Ammonium molybdate reacts with silica to form a yellow color.
Revisions	As no evaporation takes place with Autoclave 75 ml. of sample was used, instead of 100 ml. suggested in Std. methods where boiling of samples is assumed. After neutralization, samples are brought up to 100 ml. with de-ionized H_2O. Samples placed in 125 ml. Erlenmeyer flasks and duplicates run for each depth.	Extraction steps outlined in Std. methods used for increased sensitivity. Can be no residue in the Isobutyl Alcohol, as this may cause cloudiness in sample.	24 test tubes in test tube rack were heated in a H_2O bath over Burners. Sodium Arsenite Solution was not used as recommended in Std. methods.	100mm pipette used to draw sample. Procedure exactly as in Std. methods.	All reagents stored in plastic containers. 70 ml. screw-cap tubes used instead of Nessler tubes called for in Std. methods. The Sodium bicarbonate digestion step was found to be unnecessary.
Calculations	Read at 100mm light path on Spec. 70 at 625mm and converted to mg/l PO_4, reading directly from a standard curve. (0.1ppm-0.3-0.5-0.7-.10-.12ppm).	Absorbance read at 625mm through 100mm and converted to mg/l PO_4, from a standard curve, (0.1 ppm-.03-.05-.07-.10-.12ppm).	Absorbance read at 410mμ through 50mm and converted to mg/l NO_3-N, reading directly from a standard curve. (.01 mg/l-.03-.05-.07-.10-.13-.15mg/l) 3 .05 mg/l standards and blanks were run with each set of samples.	Arbsorbance read at 420mμ through 50mm and converted to mg/l SO_4. Read directly from a standard curve. (1.0mg/l-1.5-2.0-2.5mg/l).	Absorbance read at 410mm through 50mm and converted to mg/l SiO_2. Read directly from a standard curve (.20mg/l-.60-1.0-1.4-2.0mg/l).

RESULTS AND DISCUSSION

The reservoir may be viewed as a vertical series of horizontal strata, each stratum represented by a sample depth in the water column. To aid application of the data from this study, a table has been prepared which gives strata volumes as a variable controlled by depth and reservoir surface elevation (Table 4).

Appendix tables 1-5 and 7-11 present means and ranges of the water quality parameters sampled, according to the 3 strata corresponding to the average summer thicknesses of the epilimnion, metalimnion, and hypolimnion. Tables 5 and 6 present means and ranges of these same water quality parameters, but averaged over all 3 years of the study, over all stations, and over all depths.

Thermal Patterns

Each year, maximum summer surface temperatures exceeded 70 F at all stations, peaking at 80.2 F (RM 3) on August 2, 1973 (Figures 2-6). Surface temperatures generally exceeded 70 F from early July through August.

Despite the great depth of the reservoir, the epilimnion was relatively shallow, as indicated by the metalimnion midpoint never dropping below 55 ft (Figure 10). Stratification began by late April but did not attain maximum stability until August. Thermal stratification was then, very pronounced and near surface in summer. The stability of the reservoir in summer stratification was illustrated by the extremely steep temperature gradient throughout the reservoir in June-September. A typical bathythermograph plot at RM 3 showed a 19 F decline in temperature from 13 to 16 feet on July 30, 1973. All sites began thermally

Table 4. Volume (acre feet x 10^3) of depth strata in Dworshak Reservoir as a function of surface elevation.

	Pool Elevations (feet msl)																
	1600	1595	1590	1585	1580	1575	1570	1565	1560	1555	1550	1545	1540	1535	1530	1525	1520
Volume Below 0'	3468	3383	3299	3215	3131	3047	2962	2878	2794	2724	2655	2586	2516	2446	2377	2307	2238
Aft in 0-5' (x 10^3)	85	84	84	84	84	85	84	84	70	69	69	70	70	69	70	69	57
Percent of Total Volume	2.45	2.48	2.55	2.61	2.68	2.79	2.84	2.92	2.51	2.53	2.60	2.71	2.78	2.82	2.94	2.99	2.55
Volume Below 5'	3383	3299	3215	3131	3047	2962	2878	2794	2724	2655	2586	2516	2446	2377	2307	2238	2181
Aft in 5-15' (x 10^3)	168	168	168	169	169	168	154	139	138	139	140	139	139	139	126	114	114
Percent of Total Volume	4.84	4.97	5.09	5.26	5.40	6.83	7.02	7.26	7.48	7.67	7.83	5.38	5.52	5.68	5.30	4.94	5.09
Volume Below 15'	3215	3131	3047	2962	2878	2794	2724	2655	2586	2516	2446	2377	2307	2238	2181	2124	2067
Aft in 15-30 (x 10^3)	253	253	253	238	223	208	208	209	209	209	208	196	183	171	171	171	171
Percent of Total Volume	7.30	7.48	7.67	7.40	7.12	6.83	7.02	7.26	7.48	7.67	7.83	7.58	7.27	6.99	7.19	7.41	7.64
Volume Below 30'	2962	2878	2794	2924	2655	2586	2516	2446	2377	2307	2238	2181	2124	2067	2010	1953	1896
Aft in 30-40 (x 10^3)	168	154	139	139	139	70	70	69	70	69	57	57	57	57	57	57	57
Percent of Total Volume	4.84	4.55	4.21	4.32	4.44	2.30	2.36	2.40	2.51	2.53	2.15	2.20	2.27	2.33	2.40	2.47	2.55
Volume Below 40'	2794	2724	2655	2586	2516	2516	2446	2377	2307	2238	2181	2124	2067	2010	1953	1896	1839
Aft in 40-175' (x 10^3)	1502	1472	1443	1413	1382	1422	1385	1350	1313	1278	1254	1230	1207	1183	1173	1123	1094
Percent of Total Volume	43.32	43.51	43.75	43.95	44.14	46.67	46.76	46.91	49.99	46.93	47.23	47.56	47.98	48.36	49.36	48.68	48.89
Volume Below 175'	1292	1252	1212	1173	1134	1094	1061	1027	994	960	927	894	860	827	780	773	745
Aft in 175-400' (x 10^3)	1097	1066	1036	1007	977	946	923	899	875	848	822	795	768	742	702	702	680
Percent of Total Volume	31.63	31.51	31.40	31.32	31.20	31.05	31.16	31.24	31.32	31.13	30.96	30.74	30.52	30.34	29.53	30.43	30.38
Volume Below 400'	195	186	176	166	157	148	138	128	119	112	105	99	92	85	78	71	65
Aft Below 400' (x 10^3)	195	186	176	166	157	148	138	128	119	112	105	99	92	85	78	71	65
Percent of Total Volume	5.62	5.50	5.33	5.16	5.01	4.86	4.66	4.45	4.26	4.11	3.95	3.83	3.66	3.48	3.28	3.08	2.90
Maximum Depth (ft)	625	620	615	610	605	600	595	590	585	580	575	570	565	560	555	550	545

Table 4. (Continued)

	Pool Elevations (feet msl)														
	1515	1510	1505	1500	1495	1490	1485	1480	1475	1470	1465	1460	1455	1450	1445
Volume Below 0'	2181	2124	2067	2010	1953	1896	1839	1782	1736	1689	1643	1596	1550	1504	1457
Aft in 0-5' (x 10^3)	57	57	57	57	57	57	57	46	47	46	47	46	46	47	47
Percent of Total Volume	2.61	2.68	2.76	2.84	2.92	3.01	3.10	2.58	2.71	2.72	2.86	2.88	2.97	3.13	3.23
Volume Below 5'	2124	2067	2010	1953	1896	1839	1782	1736	1689	1643	1596	1550	1504	1457	1410
Aft in 5-15' (x 10^3)	114	114	114	114	114	103	93	93	93	93	92	93	94	87	79
Percent of Total Volume	5.23	5.37	5.52	5.67	5.84	5.43	5.06	5.22	5.36	5.51	5.60	5.83	6.06	5.78	5.42
Volume Below 15'	2010	1953	1896	1839	1782	1736	1689	1643	1596	1550	1504	1457	1410	1370	1331
Aft in 15-20' (x 10^3)	171	171	160	150	139	140	139	139	139	140	134	126	118	118	119
Percent of Total Volume	7.84	8.05	7.74	7.46	7.12	7.38	7.56	7.80	8.01	8.29	8.16	7.89	7.61	7.85	8.17
Volume Below 30'	1839	1782	1736	1689	1643	1596	1550	1504	1457	1410	1370	1331	1292	1252	1212
Aft in 30-40' (x 10^3)	103	93	93	93	93	92	92	94	87	79	78	79	80	79	78
Percent of Total Volume	4.72	4.38	4.50	4.63	4.76	4.85	5.06	5.27	5.01	4.68	4.75	4.95	5.16	5.25	5.35
Volume Below 40'	1736	1689	1643	1596	1550	1504	1457	1410	1370	1331	1292	1252	1212	1173	1134
Aft in 40-175' (x 10^3)	1018	998	979	959	941	917	892	866	848	831	814	796	777	755	733
Percent of Total Volume	46.68	46.99	47.35	47.71	48.18	48.37	48.49	48.60	48.84	49.20	49.54	49.87	50.14	50.19	50.31
Volume Below 175'	718	691	664	637	609	587	565	544	522	500	478	456	435	418	401
Aft in 175-400' (x 10^3)	657	634	612	589	565	547	529	513	494	474	455	435	417	403	388
Percent of Total Volume	30.12	29.85	29.61	29.30	28.93	28.85	28.77	28.79	28.46	28.06	27.69	27.26	26.90	26.80	26.63
Volume Below 400'	61	57	52	48	44	40	36	31	28	26	23	21	18	15	13
Aft Below 400' (x 10^3)	61	57	52	48	44	40	36	31	28	26	23	21	18	15	13
Percent of Total Volume	2.80	2.68	2.52	2.39	2.25	2.11	1.96	1.74	1.61	1.54	1.40	1.32	1.16	1.00	0.89
Maximum Depth (ft)	540	535	530	525	520	515	510	505	500	495	490	485	480	475	470

Table 5. Means and ranges of selected limnological parameters in Dworshak Reservoir 1972-75. All stations and all depths averaged.

Parameters	1972 Min.	1972 Mean	1972 Max.	1973 Min.	1973 Mean	1973 Max.	1974 Min.	1974 Mean	1974 Max.	1972-1975 Min.	1972-1975 Mean	1972-1975 Max.
Sample depth feet	0.0	114.64	560.00	0.0	140.39	600.00	0.0	137.16	605.00	0.0	133.97	605.00
Hour	750	1226	1730	715	1128	1530	800	1200	1700	715	1150	1730
Temperature (F)	38.30	52.67	78.90	31.80	49.17	80.20	33.00	48.57	78.00	31.80	49.32	80.20
O_2 (mg/l)	0.80	8.33	13.20	0.0	7.38	12.70	3.30	8.99	12.90	0.0	8.21	8.10
% O_2	5.50	76.55	128.70	0.0	65.59	111.00	25.00	77.12	105.00	0.0	71.95	128.70
H_2S (mg/l)	0.0	0.0	0.0	0.0	0.0	0.02	0.0	0.0	0.0	0.0	0.0	0.02
pH	5.45	6.97	8.58	5.10	7.03	9.03	5.90	7.25	8.50	5.10	7.12	9.03
CO_2 (mg/l)	0.0	6.57	47.00	0.0	8.92	46.00	0.0	5.76	24.20	0.0	7.21	47.00
Total Alkalinity (mg/l)	0.0	11.44	33.00	1.00	15.24	35.80	5.00	14.57	37.00	0.0	14.37	37.00
HCO_3 (mg/l)	0.0	11.30	33.00	1.00	15.17	35.80	5.00	14.57	37.00	0.0	14.31	37.00
Phenolphthalein Alkalinity (mg/l)	0.0	.05	4.50	0.0	0.02	2.80	0.0	0.0	0.10	0.0	0.02	4.50
Turbidity (FTU)	0.0	10.81	38.00	0.0	5.06	41.00	0.11	6.51	99.99	0.0	6.68	99.99
Conductivity (mmhos)	0.10	32.38	135.80	19.00	34.68	91.20	6.60	24.23	63.90	0.10	29.29	135.80
Conductivity (mg/l)	5.00	15.42	64.00	8.50	16.23	43.00	3.10	11.92	99.00	3.10	14.02	99.00
Secchi (feet)	2.50	9.15	22.20	5.00	11.17	22.50	1.80	13.13	26.00	1.80	11.56	26.00

Table 6. Means and ranges of selected chemical parameter, light intensity, and algal production in Dworshak Reservoir 1972-74. All stations and all depths averaged.

Parameters	1972 Min.	1972 Mean	1972 Max.	1973 Min.	1973 Mean	1973 Max.	1974 Min.	1974 Mean	1974 Max.	1972-1974 Min.	1972-1974 Mean	1972-1974 Max.
Sample depth feet	0	122	560	0	126	610	0	112	605	0	120	610
O-PO_4-P (mg/l)	0	0.032	0.44	0.01	0.014	0.114	0.01	0.016	0.048	0	0.017	0.44
NO_3 (mg/l)	0.01	0.051	0.26	0.01	0.046	0.156	0.012	0.062	0.262	0.01	0.053	0.262
SO_4 (mg/l)	1.0	1.24	7.7	0.072	1.078	1.98	1.00	1.22	2.55	0.072	1.158	7.7
Total Organic Carbon (mg/l)	1.65	3.74	8.93	0.67	2.67	24.5	0.55	2.02	6.88	0.55	2.47	24.5
Fe (mg/l)	0.1	0.11	0.33	0.1	0.11	0.7	0.01	0.099	0.1	0.01	0.103	0.7
$Si O_2$ (mg/l)	0.02	0.64	2.97	0.083	1.13	3.063	0.073	1.317	2.85	0.02	1.09	3.063
Total Phosphorous (mg/l)	–	–	–	–	–	–	0.013	0.033	0.125	0.013	0.033	0.125
Light (foot candles)	0	1145	7500	0	611	8100	0	806	9400	0	736	9400
% Surface Light	0	21.9	94.9	0	16.0	97.9	0	15.9	99.0	0	16.4	99.0
Primary Production ($MgC^{12}/m^3/hr$)	0.77	5.71	15.23	0	7.14	118.0	0	3.15	70.97	0	5.23	118.0
Total Depth (feet)	130	355	570	133	421	628	68	419	630	68	413	630

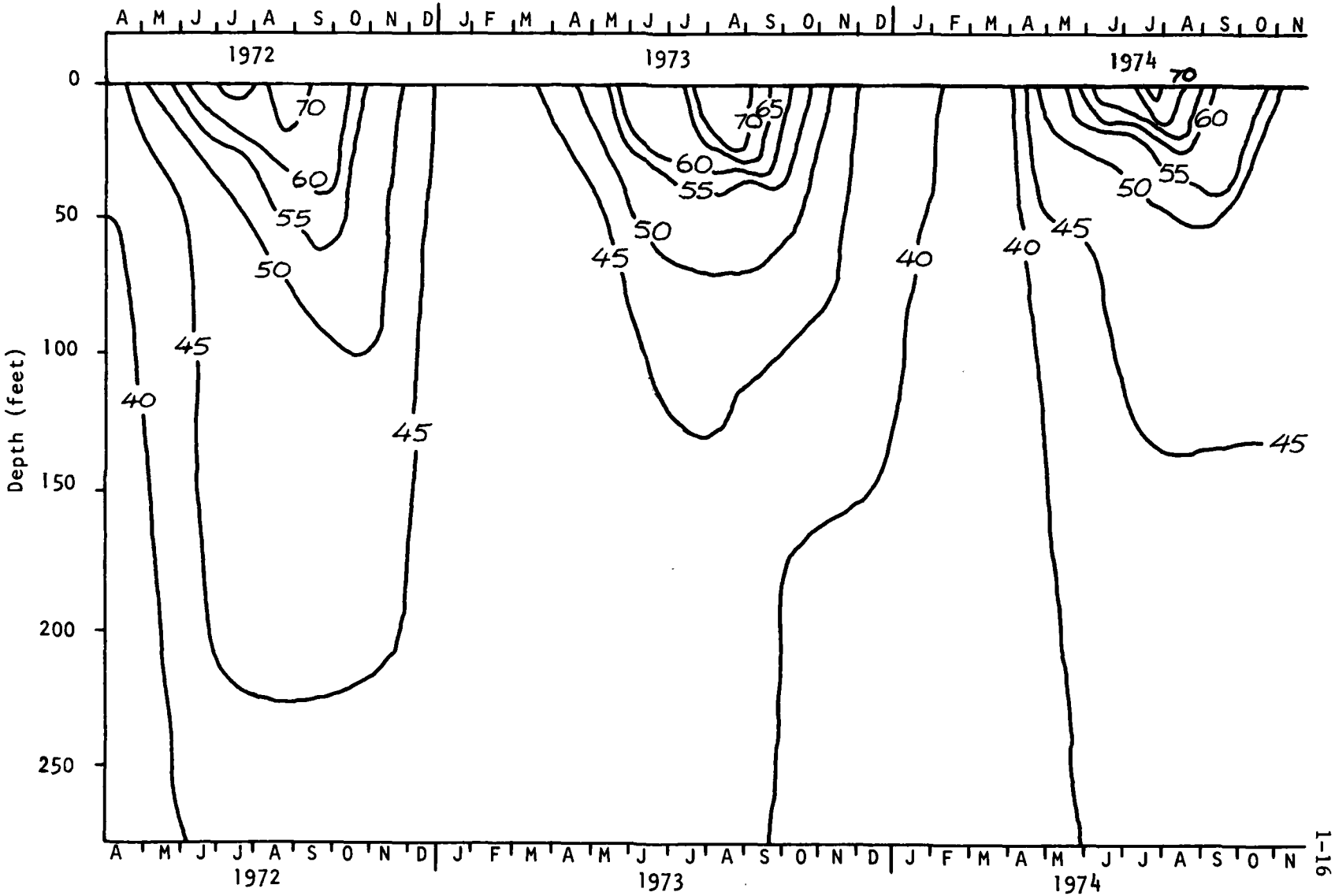


Figure 2. Temperature patterns (F) at RM 3 in Dworshak Reservoir, 1972-74.

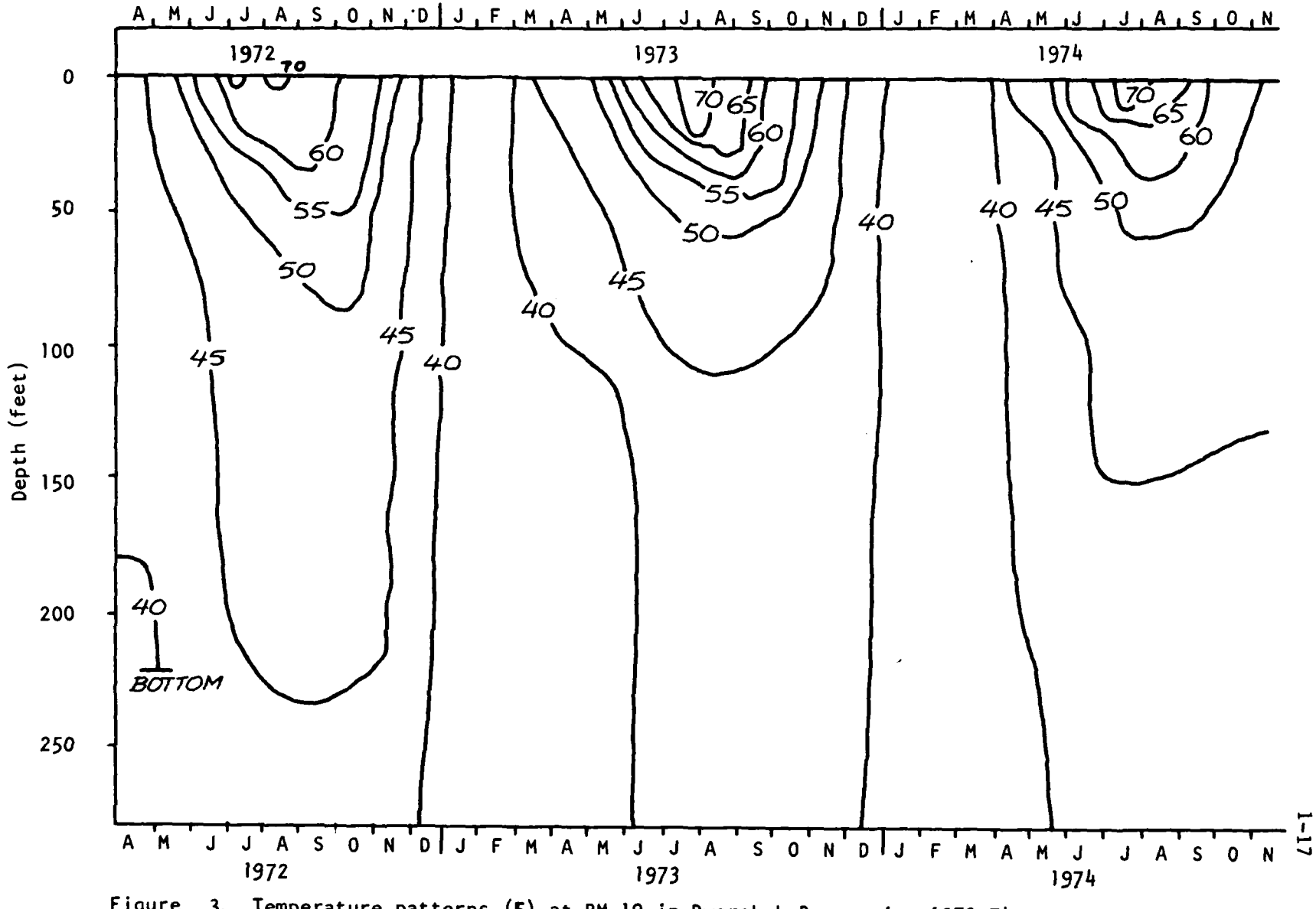


Figure 3. Temperature patterns (F) at RM 19 in Dworshak Reservoir, 1972-74.

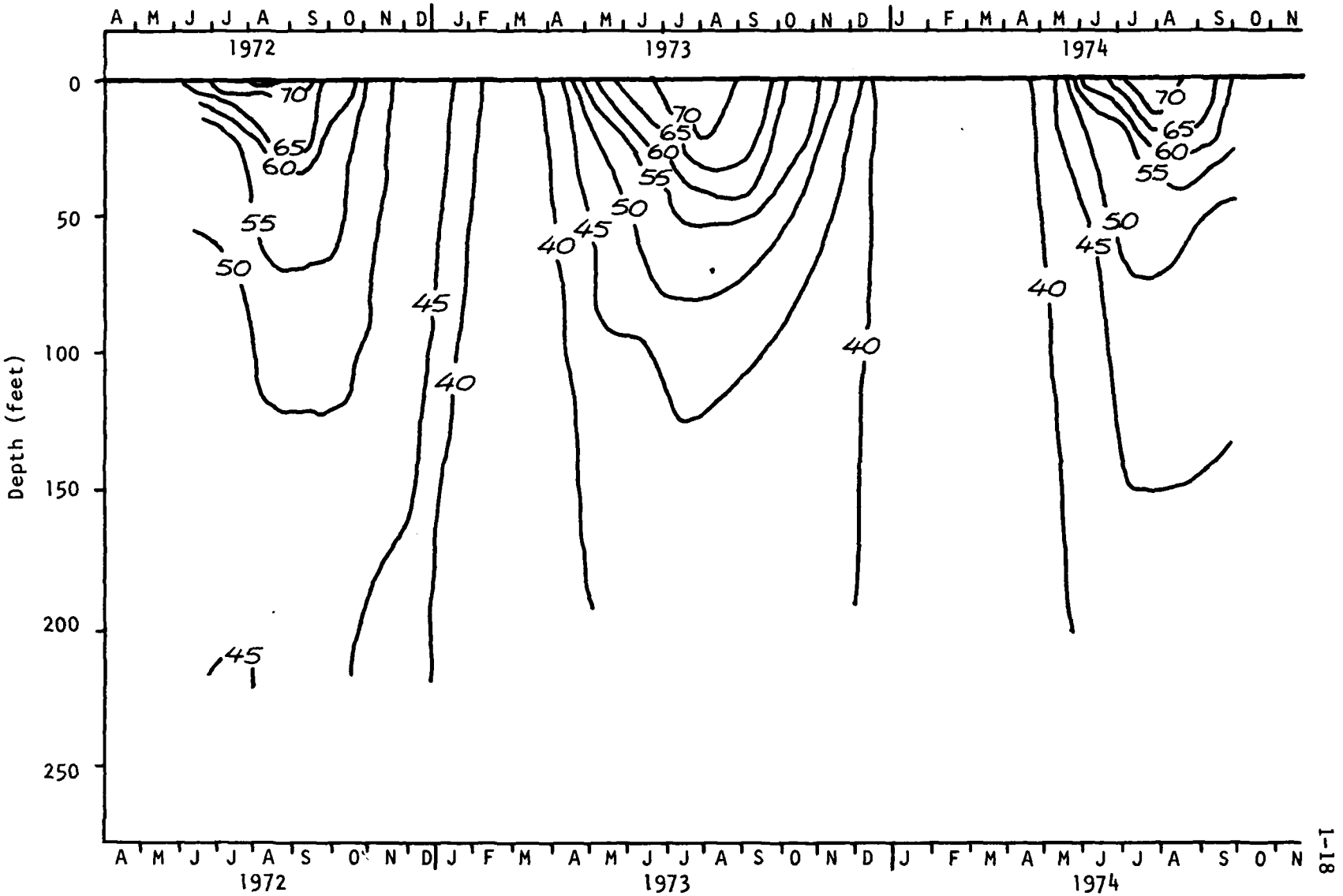


Figure 4. Temperature (F) at RM 35 in Dworshak Reservoir, 1972-74.

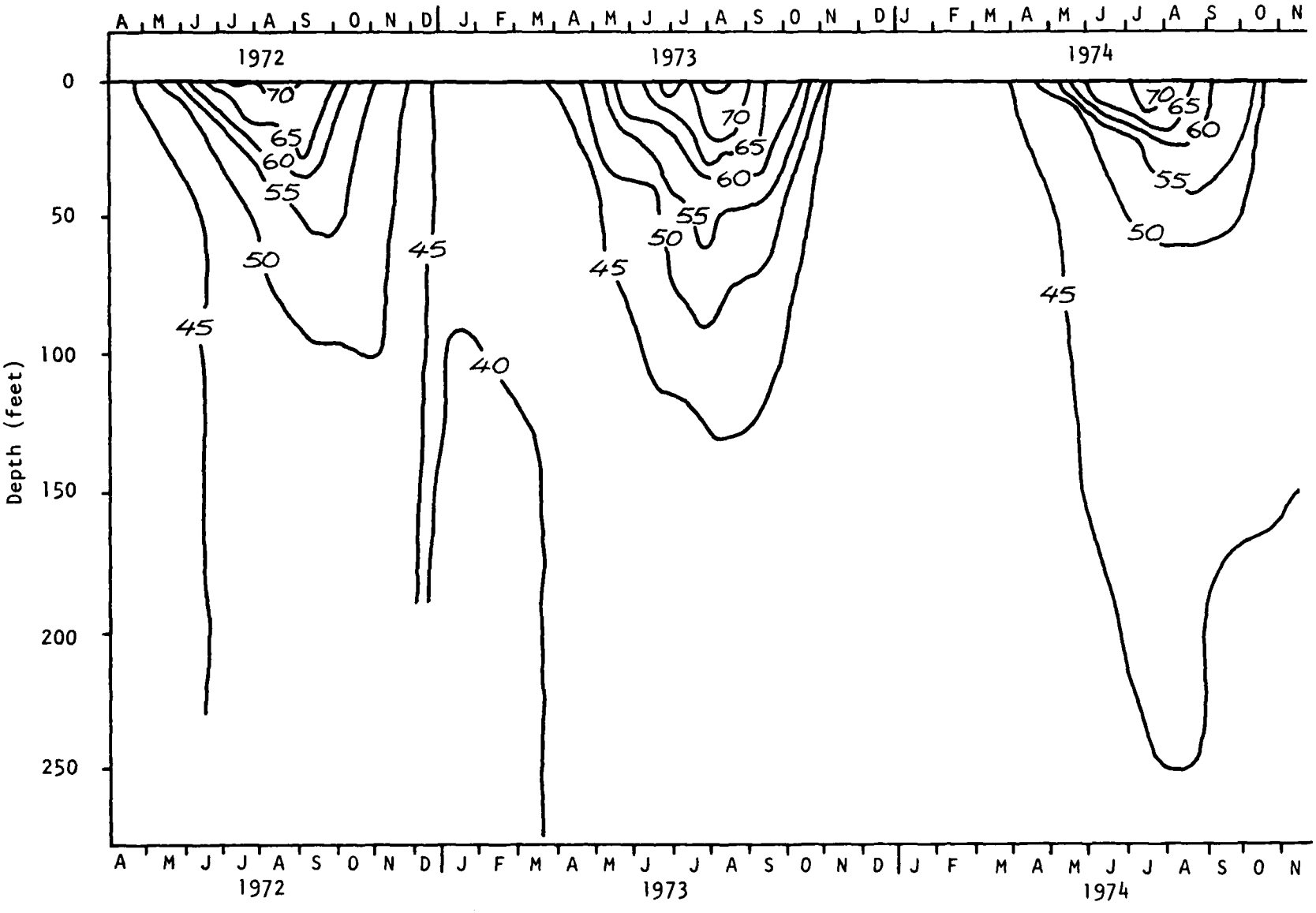


Figure 5. Temperature (F) at EC 4 in Dworshak Reservoir, 1972-74.

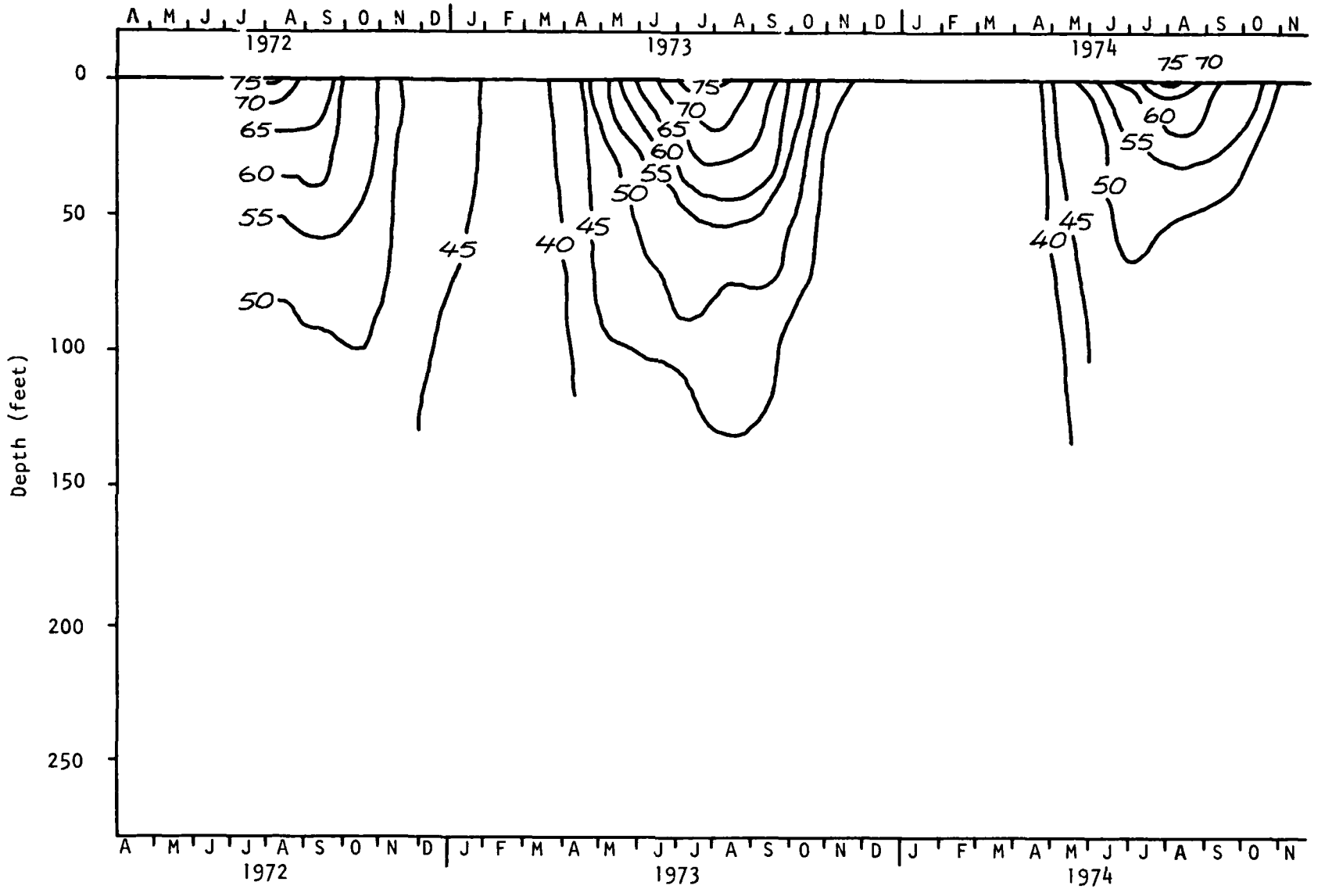


Figure 6. Temperature patterns (F) at LNFK 1 in Dworshak Reservoir, 1972-74.

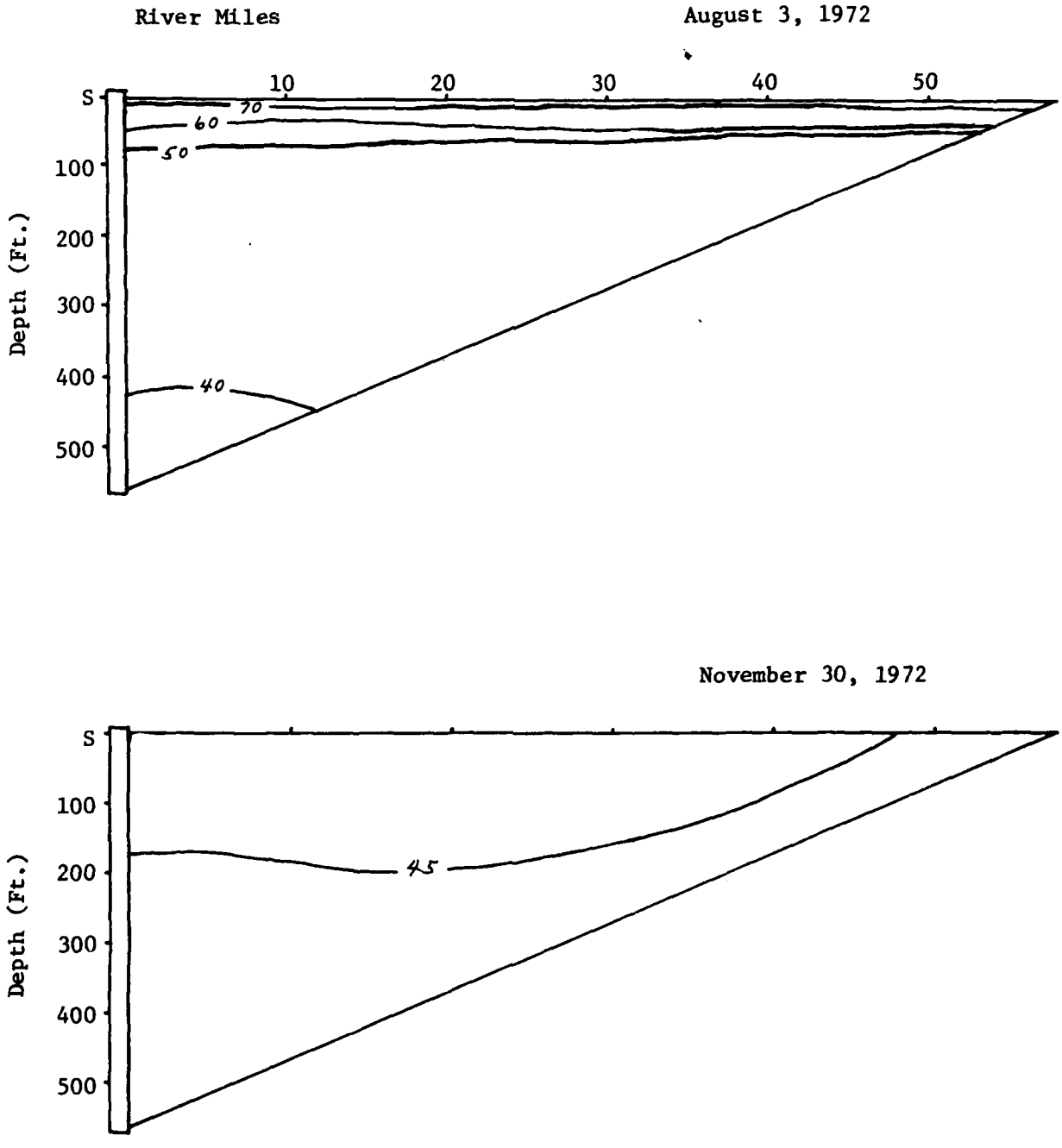


Figure 7. Longitudinal temperature profiles (F) in Dworshak Reservoir, 1972.

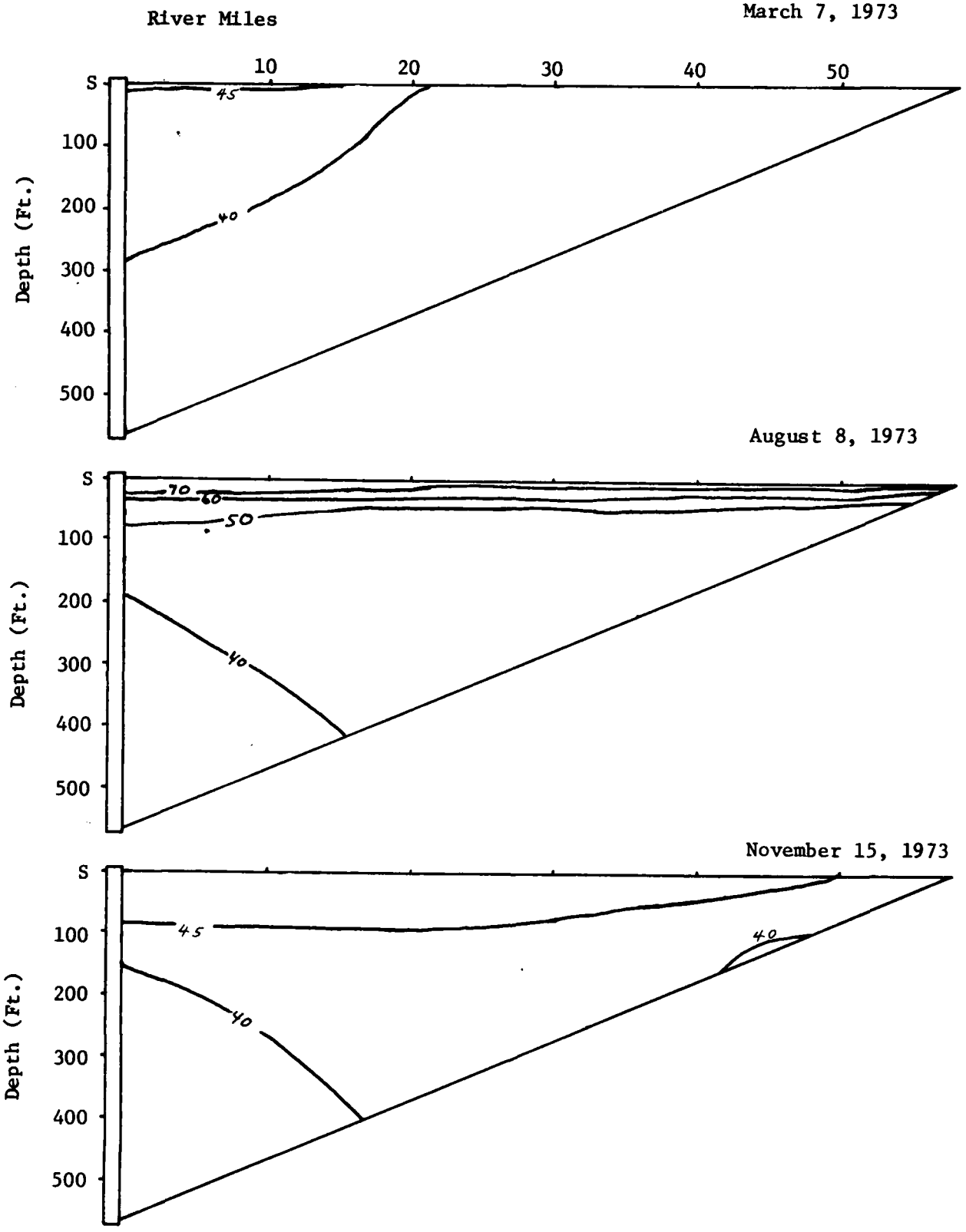


Figure 8. Longitudinal temperature profiles (F) in Dworshak Reservoir, 1973.

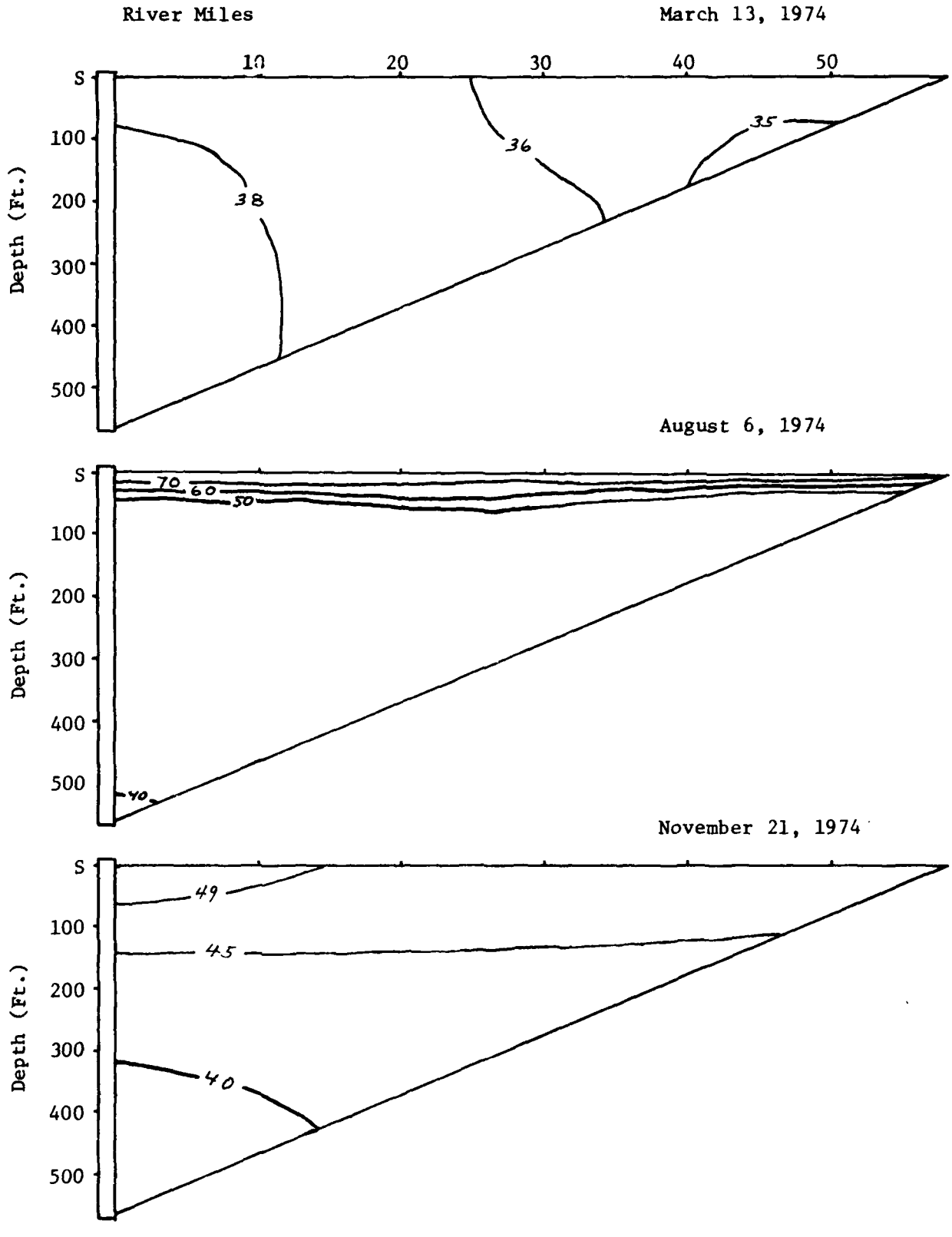


Figure 9. Longitudinal temperature profiles (F) in Dworshak Reservoir, 1974.

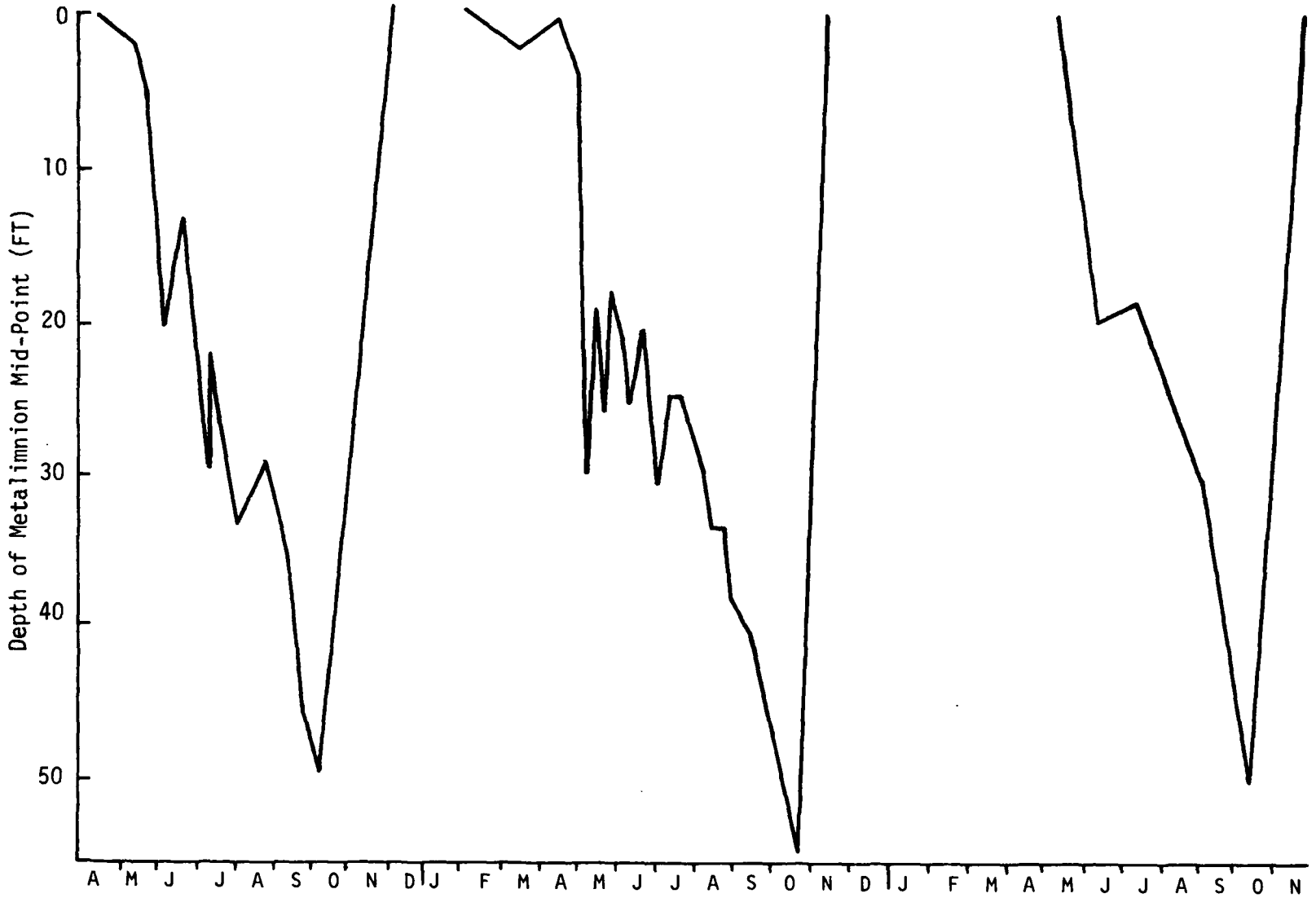


Figure 10. Depth of metalimnion midpoint in Dworshak Reservoir at RM-3, 1972-74.

stratifying at the same time, but the shallower sites began overturn approximately 2 weeks earlier than deep sites in the fall. Homothermy required 5 full months at RM 3 (attaining homothermy by late February at 39.4 F (Figure 2), but only 1 month at LNFK 1. The deeper, lower 20 miles of the reservoir is therefore monomictic, while the upper reservoir is dimictic. The upper reservoir experienced inverse stratification under ice cover but no ice formed over the lower reservoir (lower 20 miles).

Hypolimnetic waters of the lower reservoir were usually below 45 F the year round (Figures 7-9). Upper reservoir hypolimnia were usually above 45 F during summer stratification. Some cooling influence of inflows at these upper sites can be seen in Figures 7-9 with a cold underflow near the head of the reservoir sometimes obvious in March or November. Despite the winter-spring temperature lag resulting from this huge heat sink, Dworshak is a cold water reservoir. The heat distribution in August, 1973 at time of maximum heat content shows most of its contained heat in the surface 100 feet (Table 7). Water deeper than 400 feet remained below 40 F year-round.

The well defined thermal stratification permitted a choice of temperatures for downstream discharge from three locations:

- the surface 50 feet via two spillway gates;
- mid-level outlets 250 feet below the surface at full pool; and,
- variable depth penstock inlets from near the surface to a depth of 205 feet.

A comparison of mean monthly inflow and outflow temperatures shows that, without selector gate operation, reservoir discharge was much colder in summer and warmer in fall than temperatures of the inflowing North Fork

Table 7. Mean temperature per unit volume of water in Dworshak Reservoir at time of maximum heat content (August).

	1972	1973	1974
Surface - 100	61.5 F	63.0 F	55.8 F
100-200	48.3 F	45.2 F	45.0 F
200-300	46.9 F	40.8 F	42.7 F
300-400	42.9 F	40.6 F	40.5 F
400-500	39.0 F	40.0 F	39.4 F
Mean Temperature over entire reservoir (Temp/unit volume)	51.2 F	49.7 F	46.0 F

of the Clearwater (Figure 11). In August 1972, discharge waters were 16 F colder than inflow and late winter discharge was 10 F warmer than inflow. Partial selector gate operation in 1973 obtained a better matching of discharge with inflow temperatures; total selector gate operation in 1974 produced a very good matching except for in the fall. At this time there was not enough cool water in the surface 250 feet to lower discharge temperature to the cold inflow temperatures.

Summer drawoff of warm surface waters had a marked effect on reservoir heat content, especially of the surface 100 feet. Mean August temperatures of the surface 100 feet declined from 63.0 F in 1973 to 55.8 F in 1974 (Table 7). This heat difference between the two years was primarily restricted to the surface layer. Since mean annual air temperatures varied only 1.0 F between the three years, selector gate operation apparently resulted in a cooler reservoir. Near surface summer temperatures averaged 72-76 F in all years despite the differing mean temperatures of the surface 100 feet.

Water Transparency

Transparency of natural water, is a measure of the absorption of light by 3 absorption components; the absorption of light by water itself, by the solids dissolved in water, and by substances suspended in water. In Dworshak, as with most surface waters, light transmittance through water is primarily a function of the suspended particles (silts, clays, mica particles, algae, zooplankton, and detritus).

The amount of suspended particles in the water is best measured by Formazin Turbidity Units (FTU)*. Turbidity trends through the reservoir

*FTU in the 14th edition of Standard Methods was changed to NTU (Nephlometric Turbidity Units).

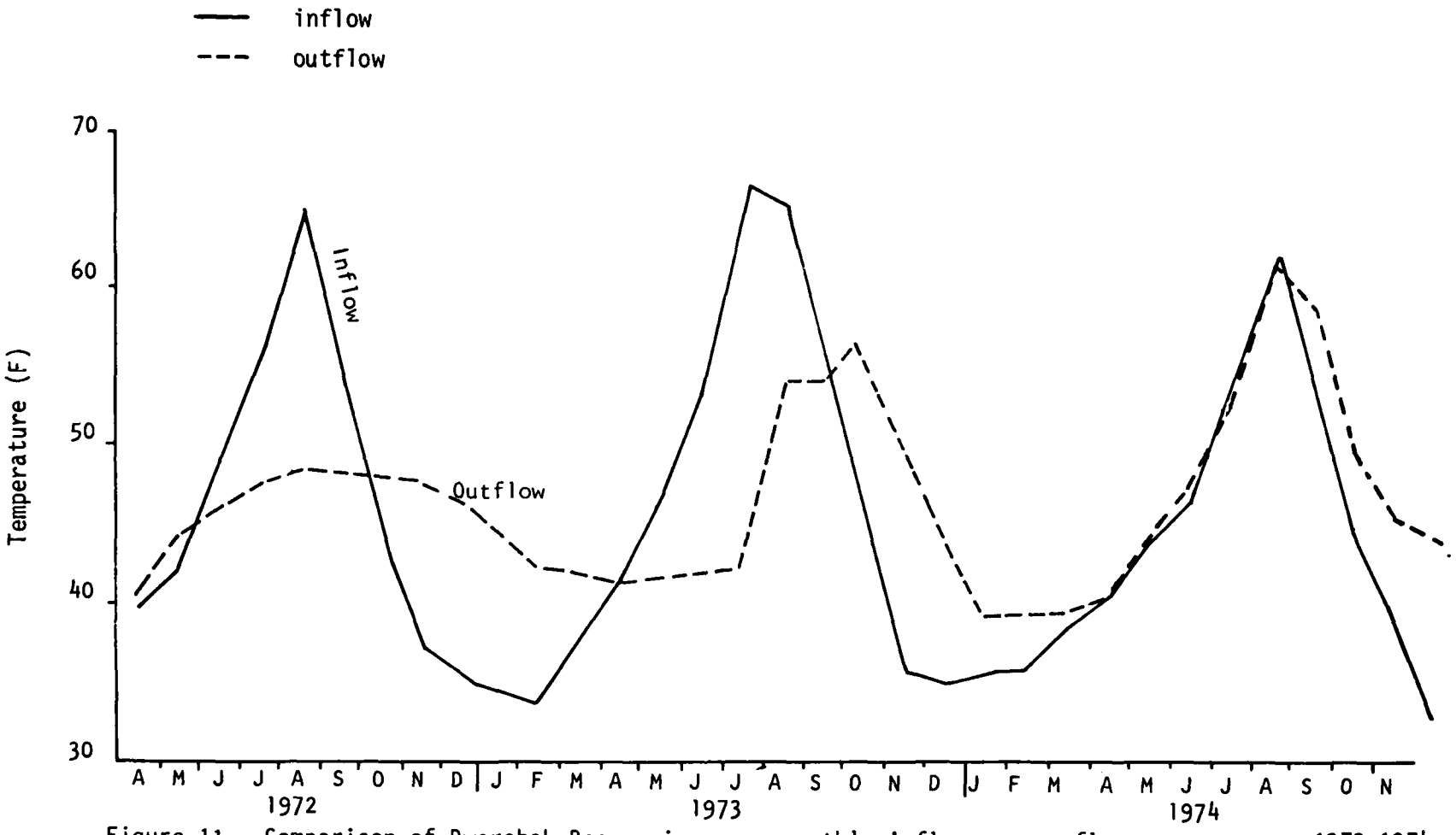


Figure 11. Comparison of Dworshak Reservoir mean monthly inflow vs. outflow temperatures 1972-1974.

during 1972-1974 are presented in Figures 12-16. Values ranged from near zero to 100 FTU, but since the extreme high values occurred in bottom waters at the deeper stations (RM 3 and RM 19), these high values are not seen in the epilimnial averages. In epilimnial waters, four annual high turbidity points were observed, but any one year might not have all four:

1) A peak of inorganic solids in high runoff, typically occurring anywhere from January to May with the varying timing of peak runoff events;
2) A turbidity peak comprised of the spring diatom bloom. This peak occurred in March-April and usually was of smaller intensity than the other two;
3) The mid-summer phytoplankton bloom; and,
4) The fall phytoplankton bloom usually occurring in September-October.

In 1972, the fall bloom phenomenon dominated turbidity patterns in the lower reservoir but not at the upper two stations. In 1973, the summer bloom dominated turbidity again in the lower reservoir, but not at the upper three stations, while in 1974 late winter inorganics dominated epilimnial turbidity patterns throughout the reservoir above RM 10. The lower reservoir spring turbidity peak was principally silt-caused also, but occurred two months later in April.

From February-May, 1974 high volume muddy inflows brought high turbidity waters into a pool drawn >120 feet below the full level. The steep water-logged banks suffered severe slumping while tributary streams and rill erosion over these exposed mud banks further contributed sus-

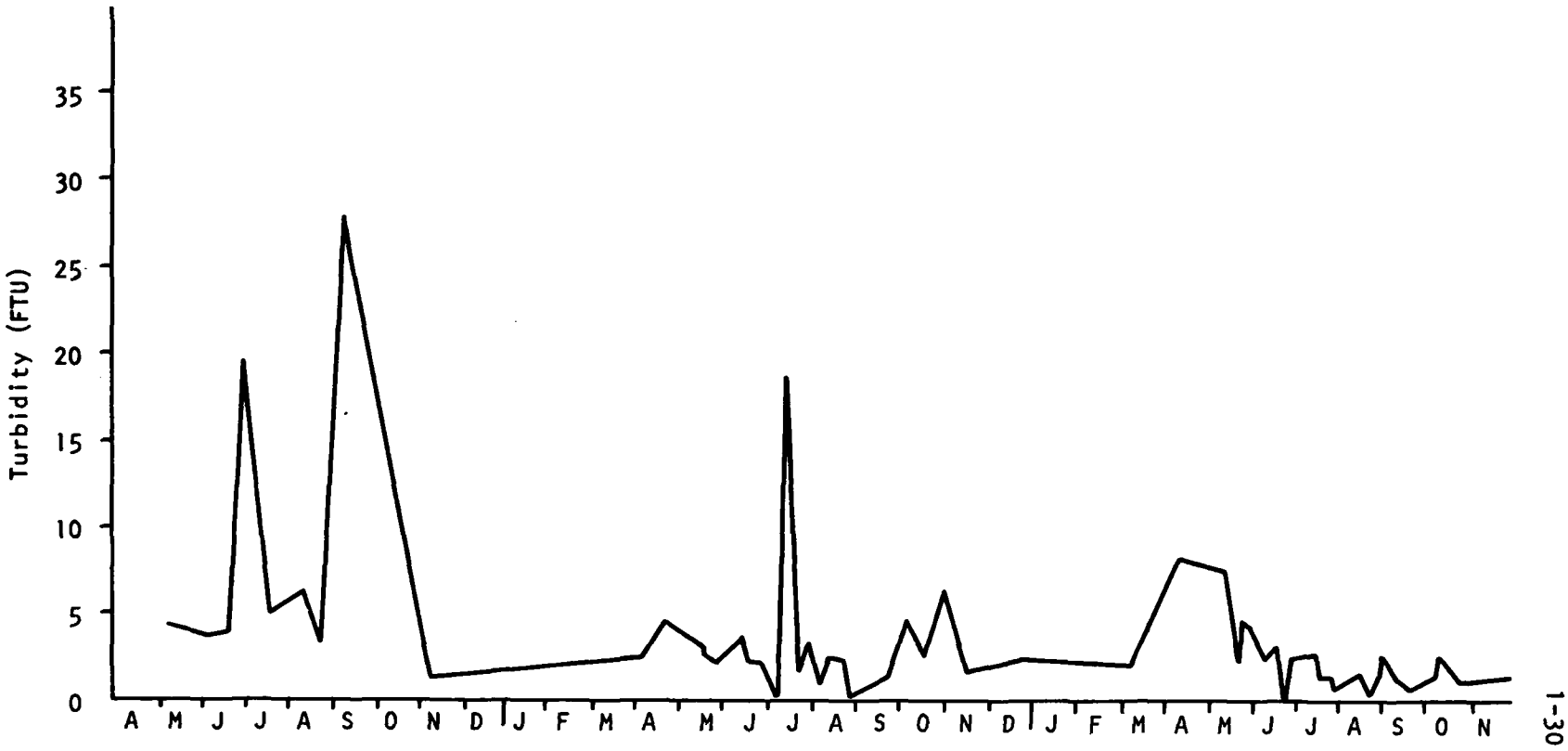


Figure 12. Turbidity (FTU) at RM 3 in Dworshak Reservoir, 1972-74 (0-40 foot averages).

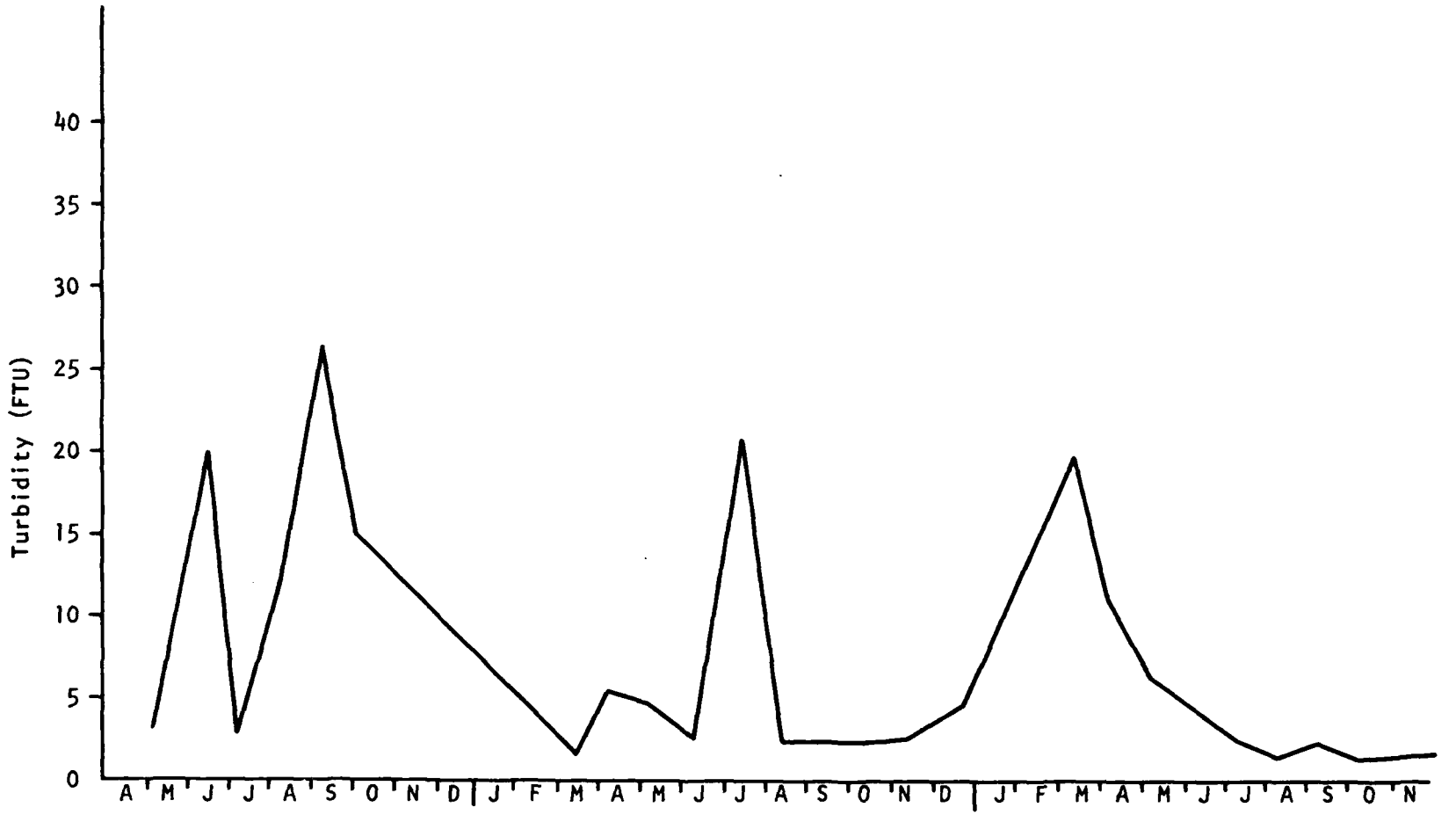


Figure 13. Turbidity (FTU) at RM 19 in Dworshak Reservoir, 1972-74 (0-40 foot averages).

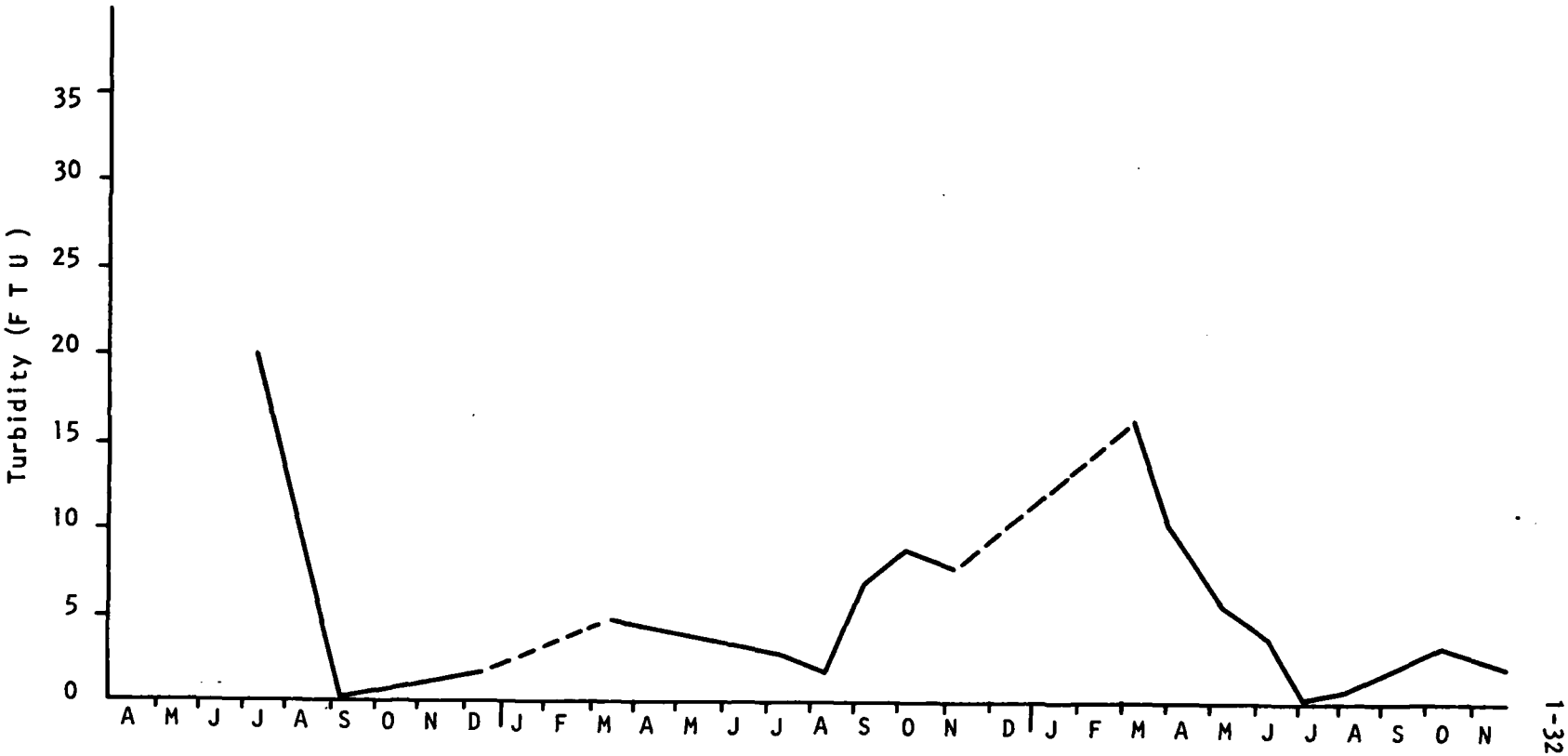


Figure 14. Turbidity (FTU) at RM 35 in Dworshak Reservoir, 1972-74 (0-40 foot averages).

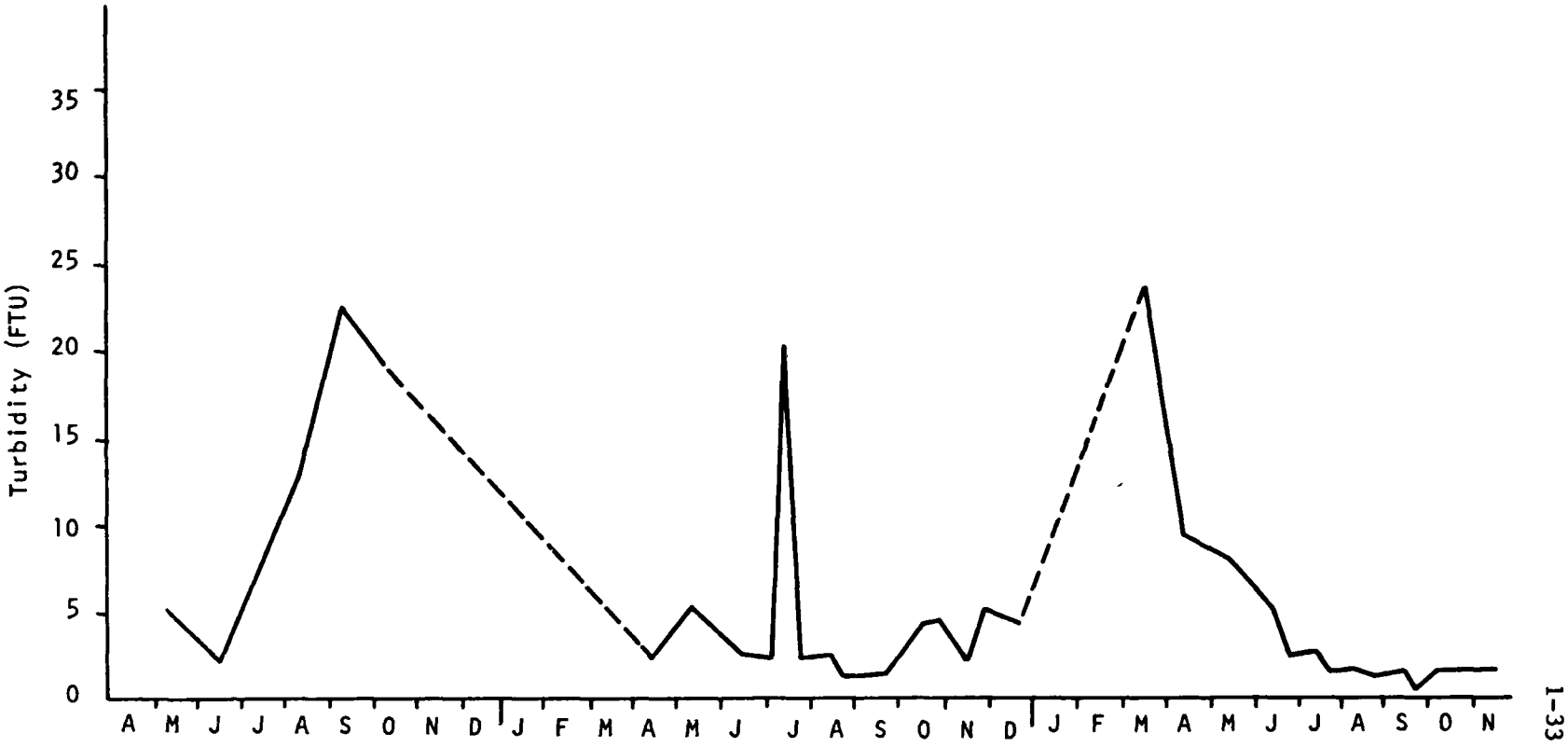


Figure 15. Turbidity (FTU) at EC 4 in Dworshak Reservoir, 1972-74 (0-40 foot averages).

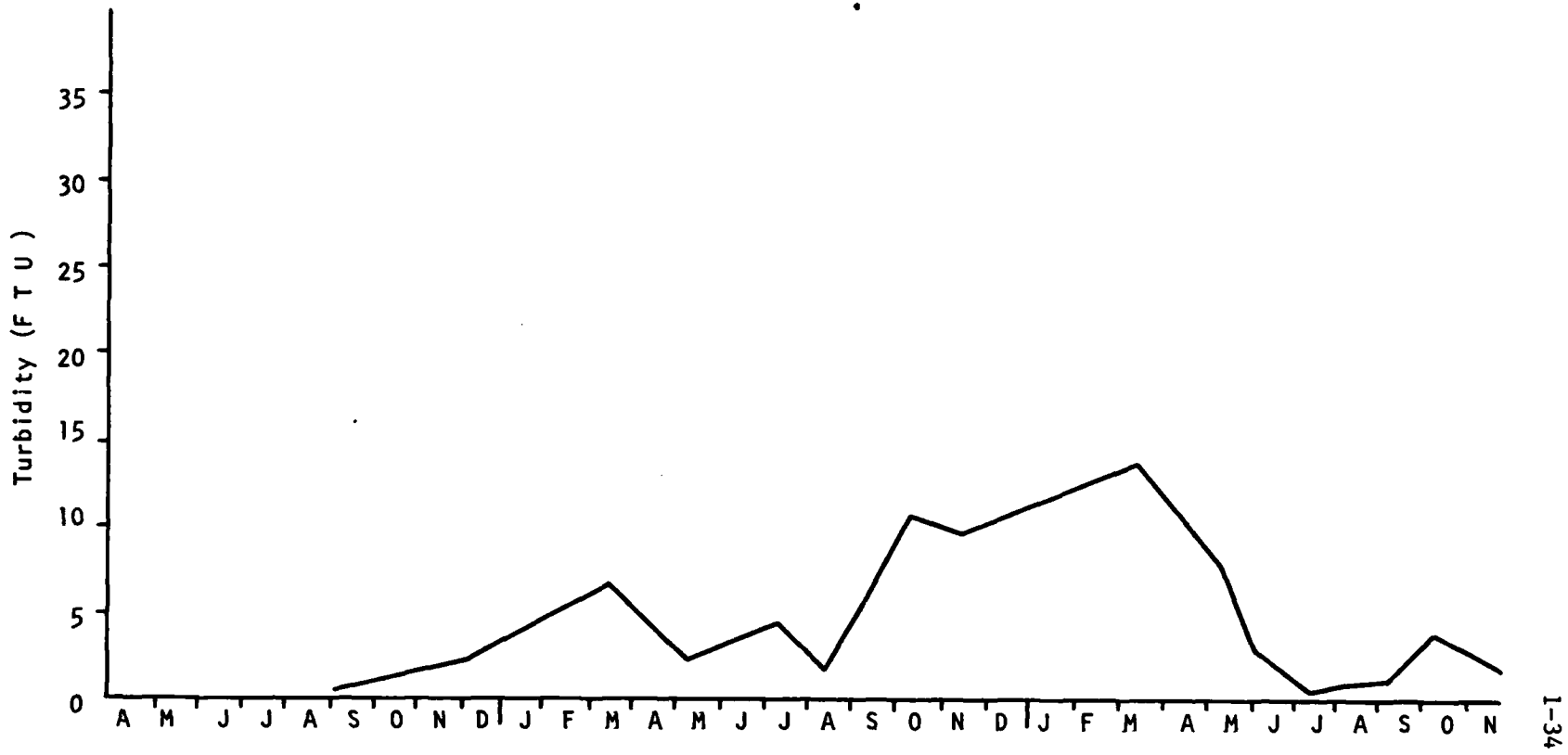


Figure 16. Turbidity (FTU) at LNFK 1 in Dworshak Reservoir, 1972-74 (0-40 foot averages).

pended solids to the water column. Gradual drawdown continually presented "new" mud shorelines to the washing action of waves. Suspended solids from these tributary and shoreline sources sank to the reservoir bottom as density currents contributing to already high deep water turbidity levels. Wave action on bare, newly exposed side and bottom sediments was a continuing source of turbidity to the water. Aerial photography documented a turbid in-shore band of water commonly streaming out from wave-washed peninsulas before sinking. Each incremental drop in water level exposed a new band of bottom sediments to wave action. As a result, spring turbidity levels in the middle reservoir surface waters were 15-20 FTU from early March through April, 1974.

Early spring inflows from the North Fork at 10-12 FTU were turbid, but were neither turbid enough nor of enough volume to contribute 97, 44, and 100 FTU's to bottom waters at RM 35, RM 19, and RM 3 by mid-March. At RM 35 and RM 19, turbidity of the entire water column approximated North Fork levels; the volume of turbid water in the reservoir by mid-March (~2.5 x 10^6 Acre Ft.) greatly exceeded estimated volumes of North Fork and Little North Fork turbid water inflows during that late winter-spring period (~1.2 x 10^6 Acre Ft.). Small tributaries did not contribute a large amount of turbidity to the reservoir in this period. These small granitic watershed streams clear rapidly after a heavy runoff so these high turbidity but short duration tributary sources contribute less than peakflow data would indicate.

The in-reservoir turbidity sources of late winter slumping and wave action on shorelines, however, were continuing sources. The extreme drawdown of February-March, 1974 aggravated both of these sources. Main

tributaries were further discounted as the predominant turbidity source by the absence of a continuous deep high turbidity density current through the reservoir in early spring, 1974. High turbidity sites were discontinuous through the reservoir.

Secchi disc transparency reflects these turbidity trends; namely, minimum transparency of the 3 year study in early spring, 1974 and a trend of increasing summer transparency from 1972 through 1974 as productivity declined (Figures A-1 through A-5, and 17; Table 8). Mean summer secchi disc depth increased through the three year study.

Relative attenuation of light as it passes through the water column is expressed graphically by a plot of percent incident light on a logrhythmic scale against increasing depth (Figures 18-22). Light absorption with passage through the water column is inversely related to the slope of the resulting line on a semi-log plot. These plots, which represent average light transmission characteristics for the spring and summer-fall periods of each year, again show greatest light absorption in spring, 1974 at all stations except LNFK 1, again indicating that major tributary turbidity inputs were not an abnormally high source of turbidity in 1974. Spring turbidity resulted in generally flatter light penetration curves than did curves for summer-fall. Summer-fall light transmission increased through the three year study at all five stations, reflecting declining planktonic production.

The vertical extinction coefficient, the percent light absorbed by each meter of water, is a single number index of total light absorption by a water column. It is low in transparent waters and high in turbid waters. Mean VEC values for each station through the study are presented

Table 8. Minimum and maximum secchi disc in Dworshak Reservoir, 1972-74.

	1972		1973		1974	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
RM 3	July 10	Nov. 2	May 3	July 26	May 14	July 16
RM 19	July 11	Sept. 6	May 3	Sept. 5	Apr. 3	Aug. 7
RM 35	June 3	Dec. 3	Mar. 11	July 15	Apr. 2	Aug. 8
EC 4	July 11	Sept. 6	May 3	July 26	Apr. 5	Aug. 20
LNF 1	-	Dec. 3	Nov. 17	July 14	Apr. 2	Aug. 8

Table 9. Mean vertical extinction coefficients in Dworshak Reservoir, 1972-74.*

		RM 3	RM 19	RM 35	EC 4	LNFK 1
1972	Spring	-	-	-	-	-
	Summer-fall	0.64	0.71	0.72	0.89	0.57
1973	Spring	0.76	0.65	0.85	0.78	0.64
	Summer-fall	0.61	0.73	0.62	0.71	0.69
1974	Spring	1.10	1.32	1.97	0.78	1.19
	Summer-fall	0.56	0.49	0.48	0.53	0.60

*Vertical Extinction Coefficient = $\frac{\ell n\, I_o\, (\Sigma z) - \Sigma[z(\ell n\, I)]}{\Sigma z^2}$

where ..... I_o = light intensity at surface
I = light intensity at depth 2
z = depth

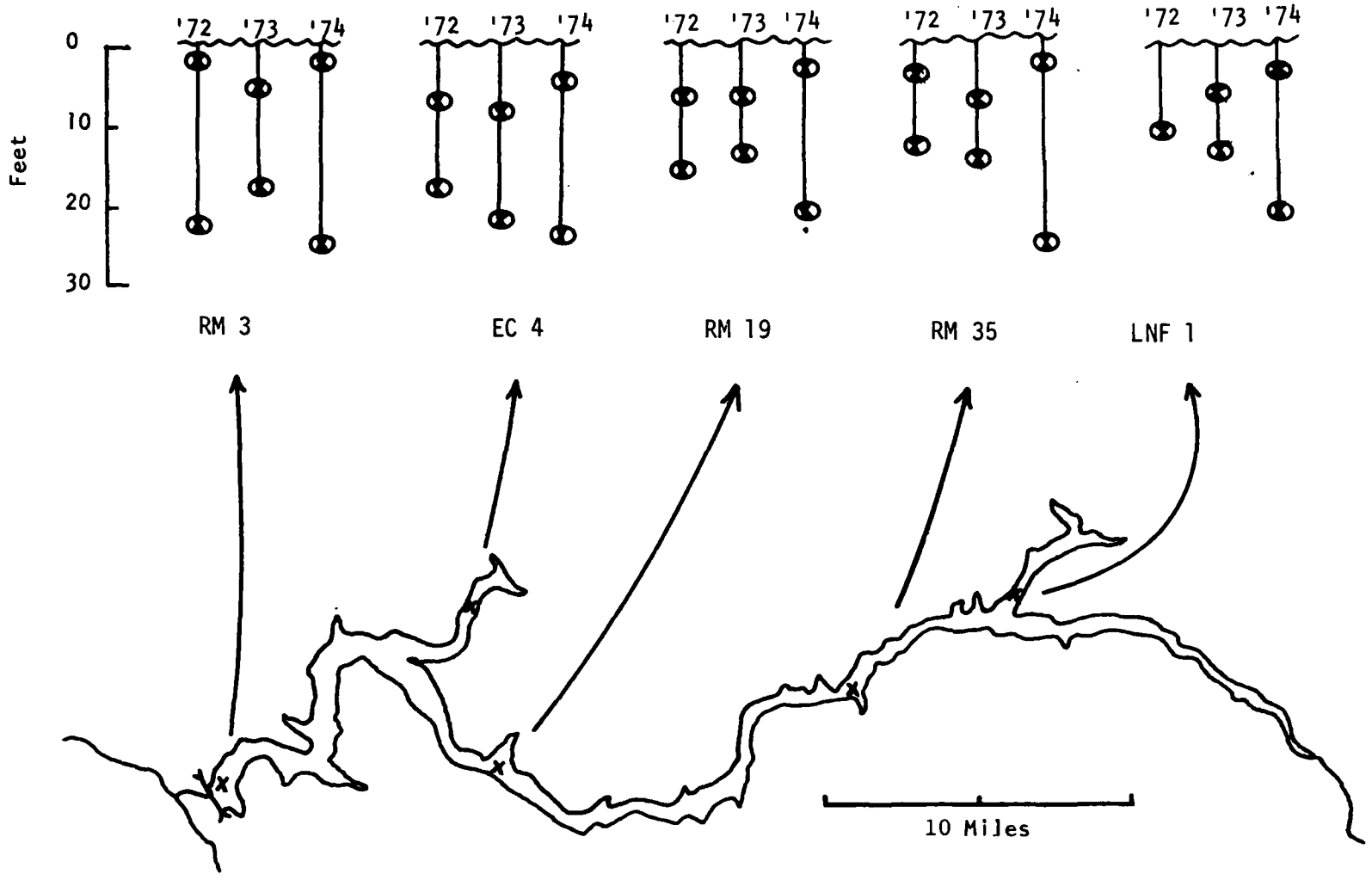


Figure 17. Annual minimum and maximum secchi disc transparency at 5 stations in Dworshak Reservoir, 1972-74.

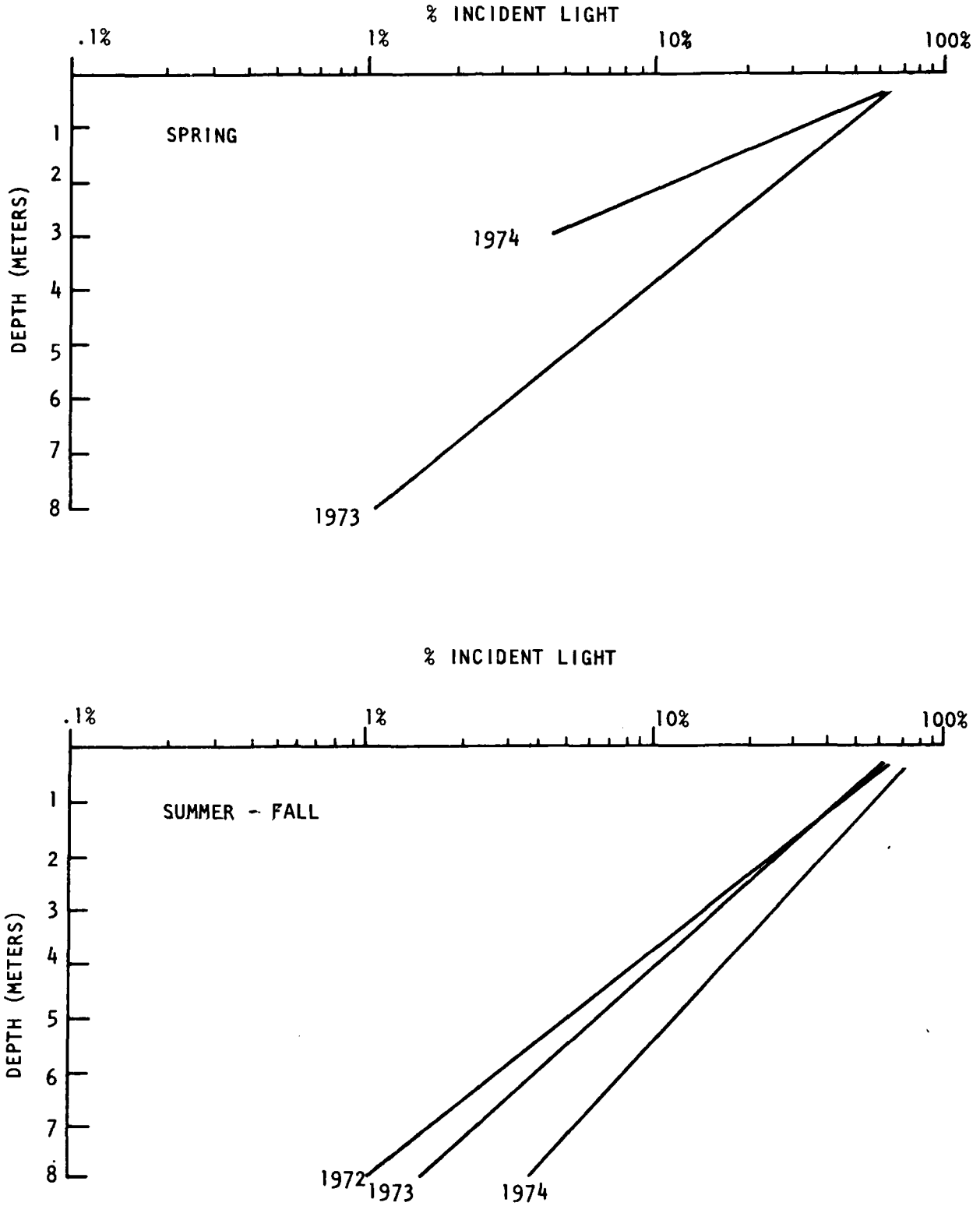


Figure 18. Average subsurface light penetration in the Spring and Summer-Fall at RM 3 in Dworshak Reservoir, 1972-74.

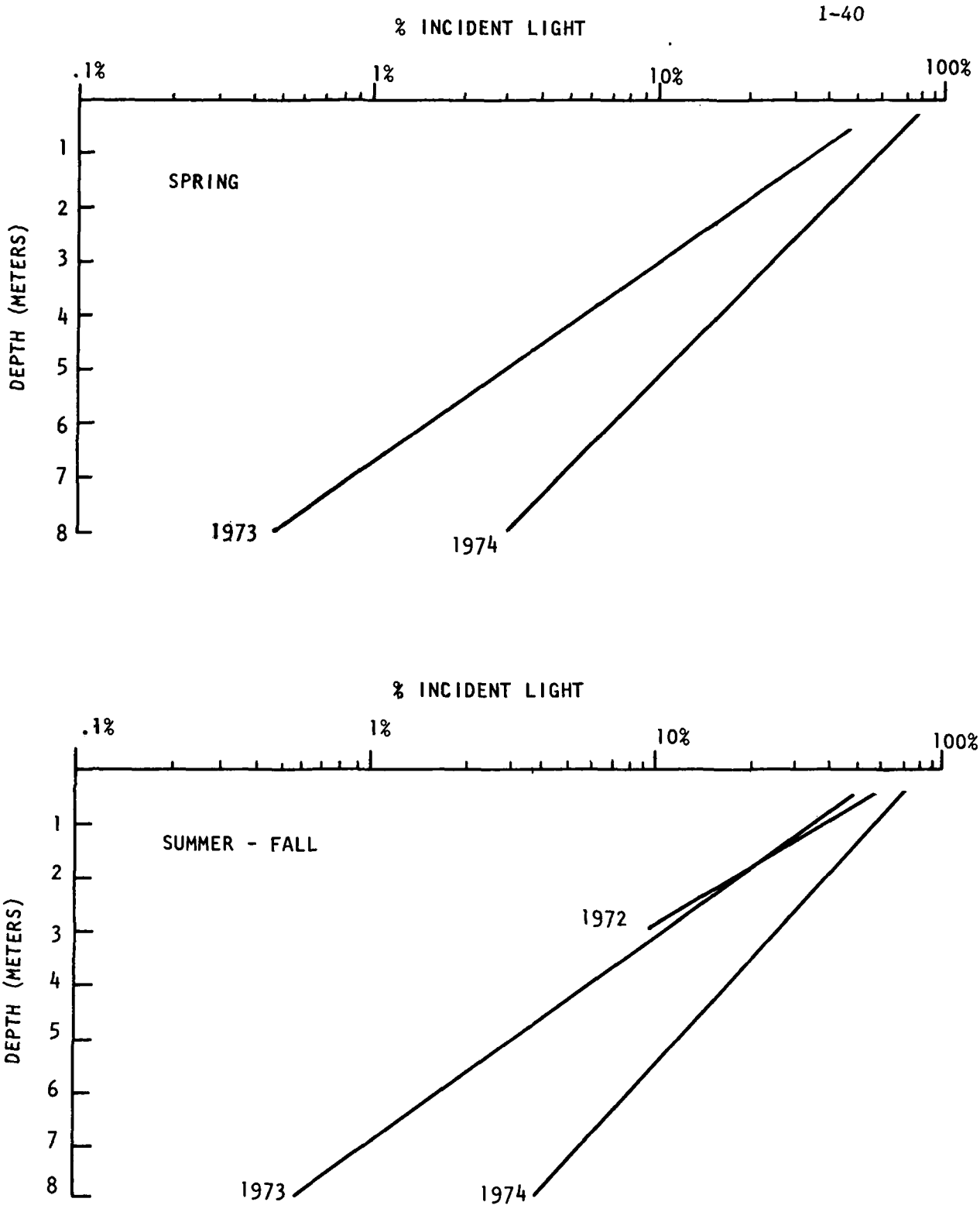


Figure 19. Average subsurface light penetration in the Spring and Summer-Fall at RM 19 in Dworshak Reservoir, 1972-74.

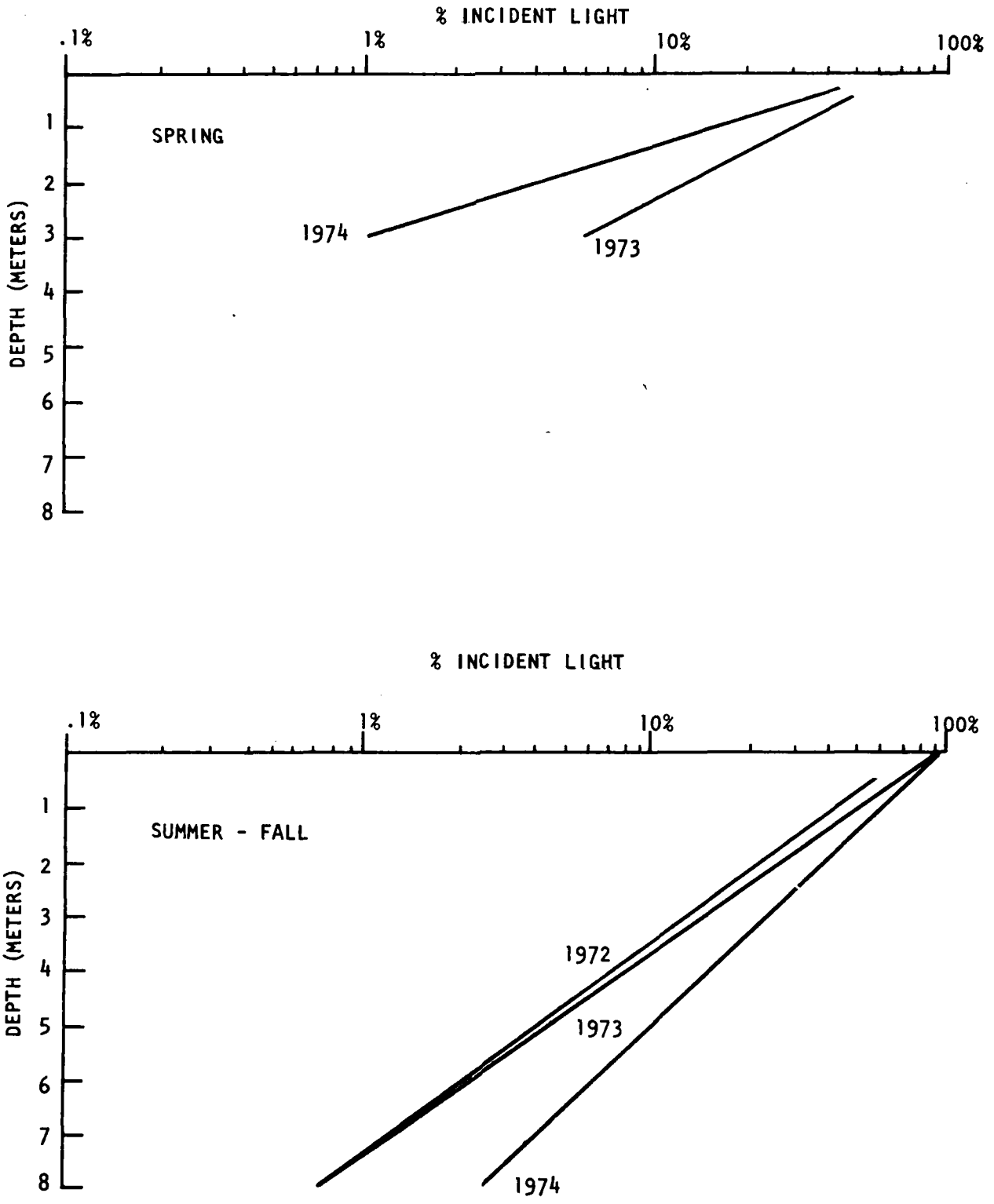


Figure 20. Average subsurface light penetration in the Spring and Summer-Fall at RM 35 in Dworshak Reservoir, 1972-74.

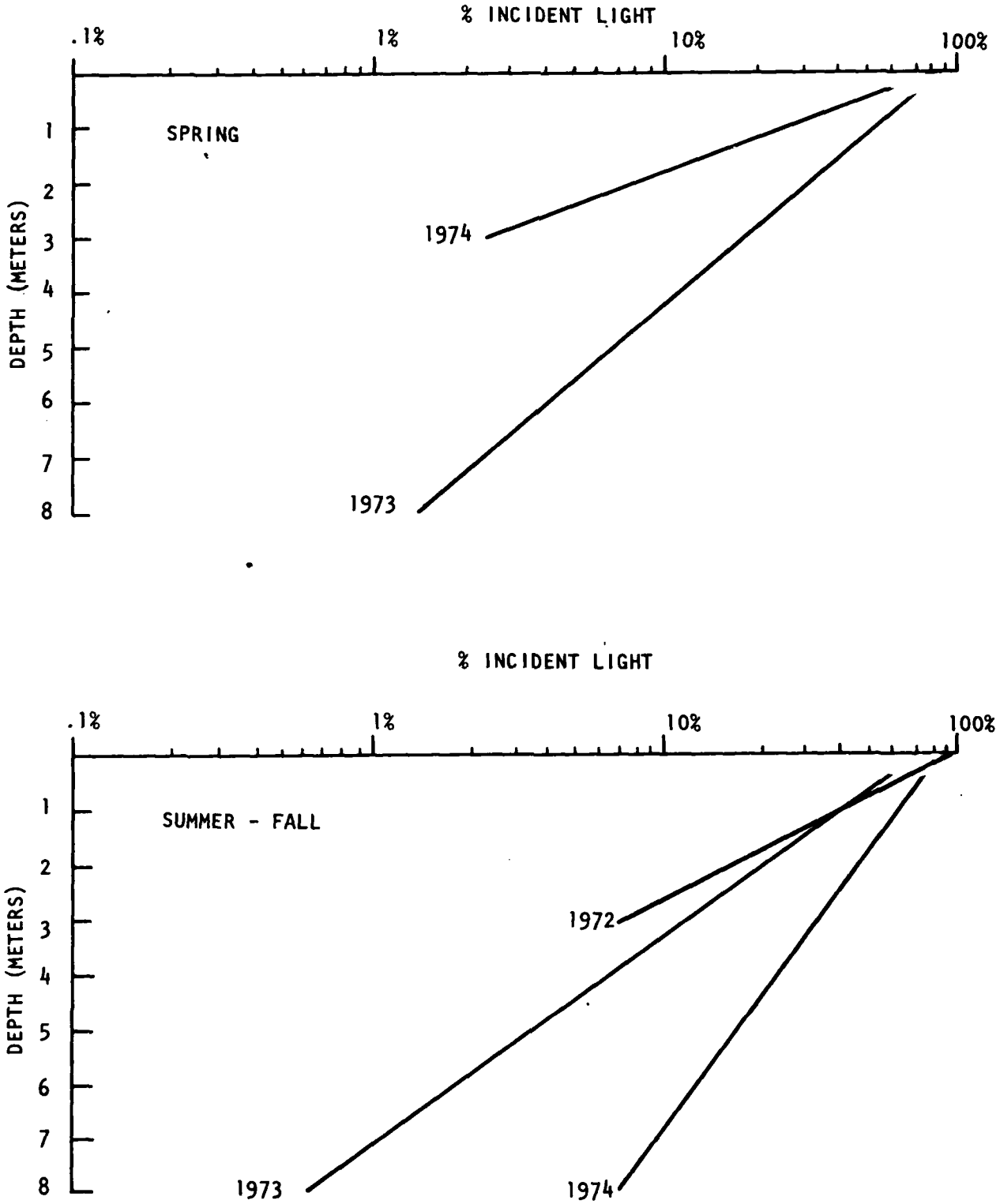


Figure 21. Average subsurface light penetration in the Spring and Summer-Fall at EC 4 in Dworshak Reservoir, 1972-74.

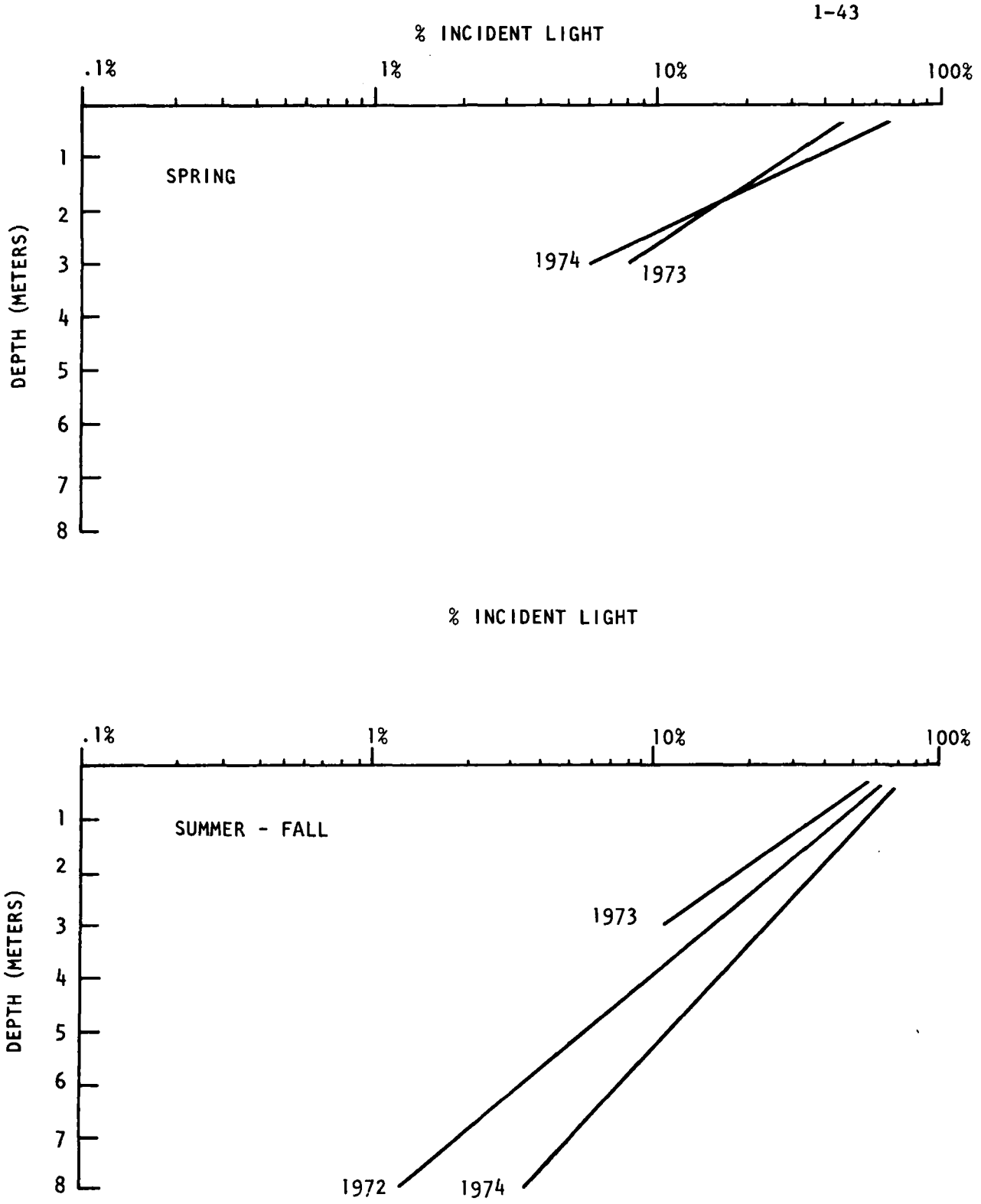


Figure 22. Average subsurface light penetration in the Spring and Summer-Fall at LNFK 1 in Dworshak Reservoir, 1972-74.

in Table 9 with individual values in Table A-6.

Dissolved Oxygen

Time-depth trends of dissolved oxygen at each station (Figures 23-27) show surface oxygen concentrations were near saturation through the summer at all stations. Some metalimnetic declines to 5-6 mg/1 were seen in late summer of 1972-1973 at RM 3 and EC 4 as a result of high epilimnial algal production.

Oxygen depletion to 0 was only observed below 500 feet in March-December, 1973. These low oxygen values resulted when deepwater oxygen demand exceeded the rate of resupply. Intense decomposition of allocthonous organic matter from floating saw timber, slash, and newly submerged soils/vegetation combined with the high algal production of 1972-1973 produced oxygen utilization rates in excess of oxygen recharge to very deep waters. The result was deepwater oxygen depletion even during circulation in periods of winter homothermy. Lower solubilization of BOD and lower algal production was evident in 1974 when 3.3 mg/1 was the lowest oxygen concentration obtained, even in deepwaters. Most 1974 observations exceeded 7.0 mg/1 oxygen.

Organic inputs and algal production were high enough in 1972 at EC 4 to result in 0.9 mg/1 oxygen below 150 feet in September-October (Figure 26). Lows in 1973 were ~4 mg/1 both below 170 feet and in the metalimnion, but 1974 produced no significant oxygen depletion at EC 4. Other stations experienced late summer deepwater oxygen depletion to 2-4 mg/1 in 1972-1973, but not in 1974. Longitudinal oxygen profiles, offering an "instantaneous" view of the entire reservoir at a point in time effectively illustrate these same oxygen trends (Figures 28-30).

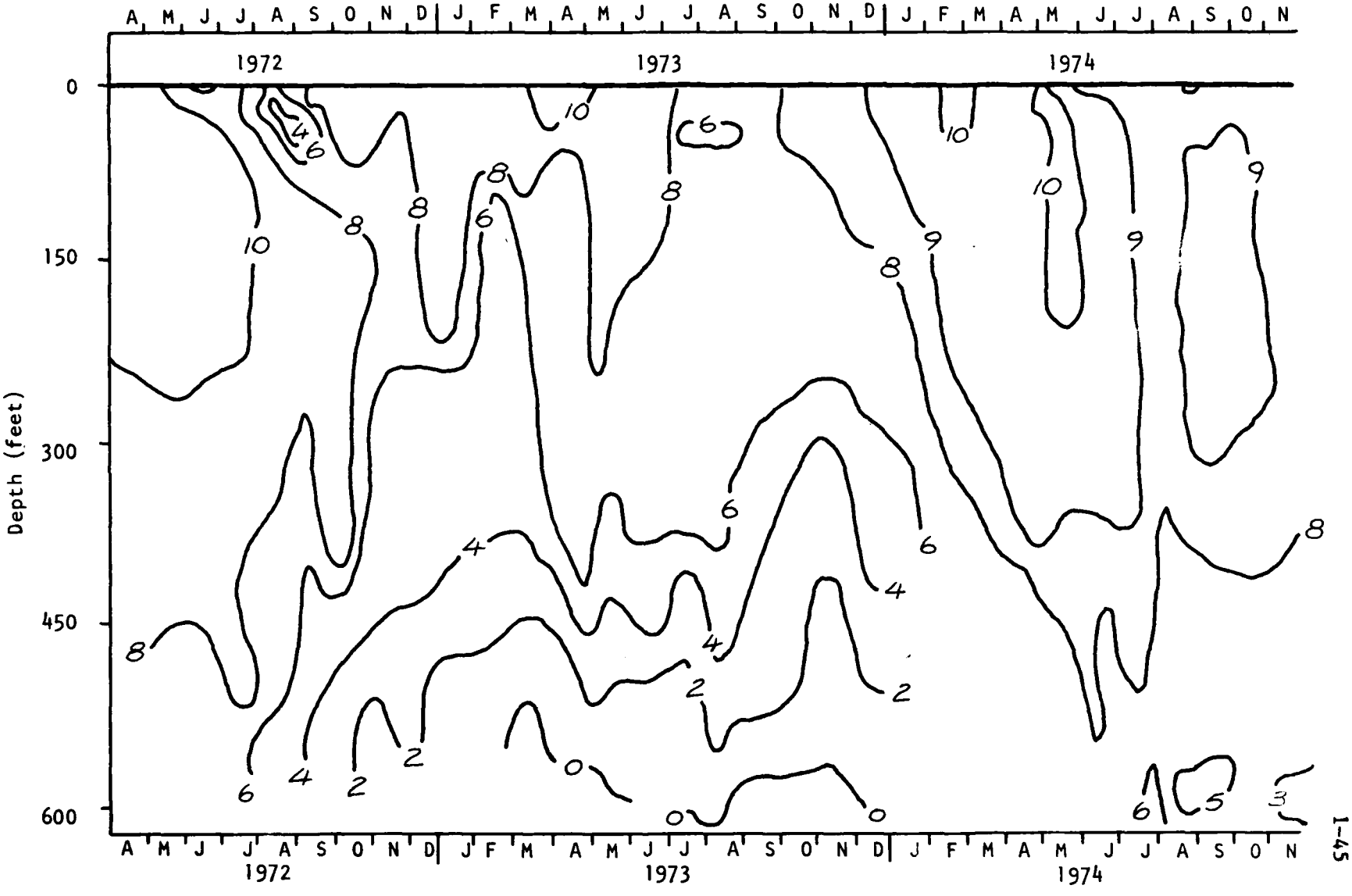


Figure 23. Dissolved oxygen (mg/l) at RM 3 in Dworshak Reservoir, 1972-74.

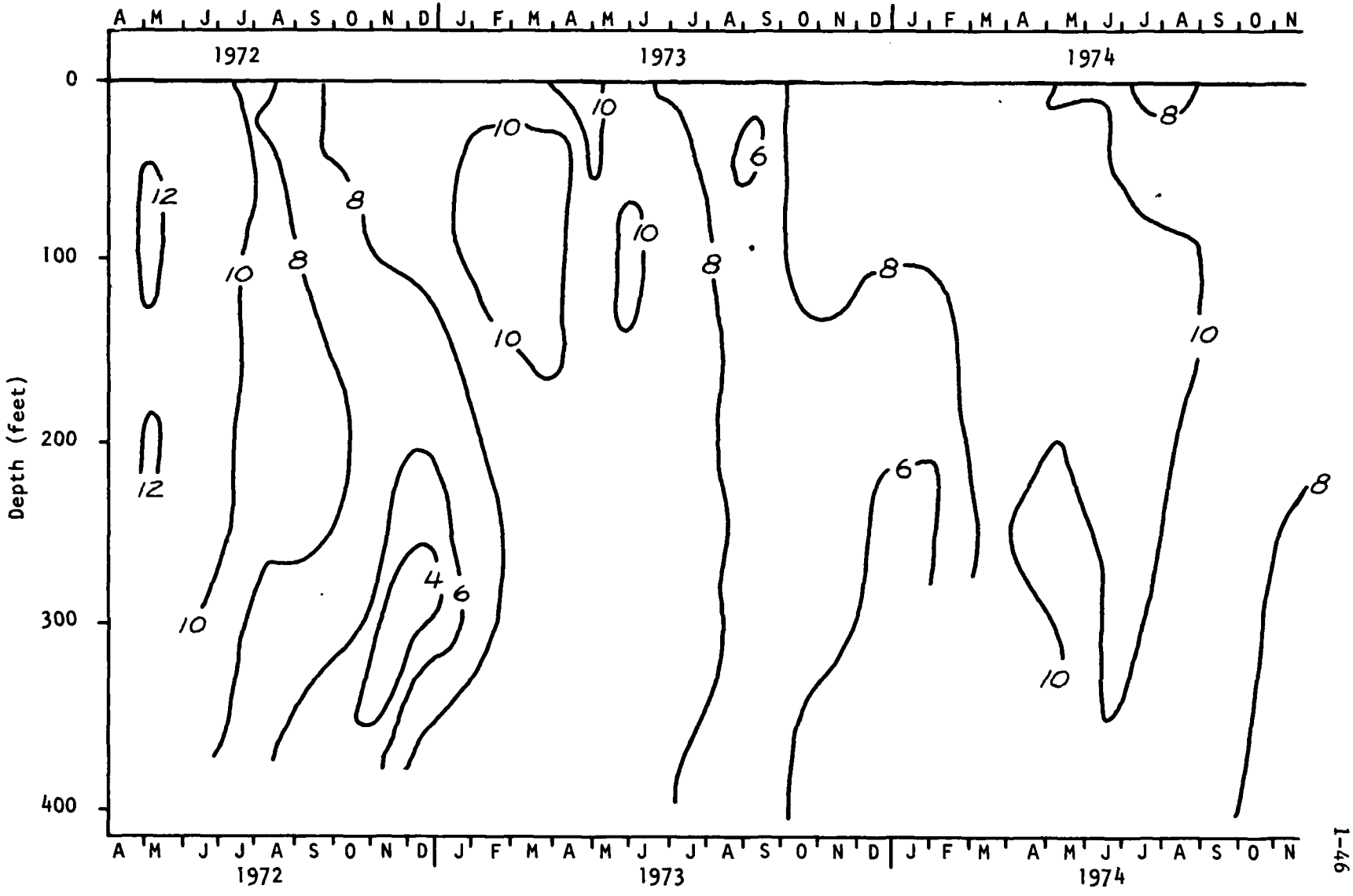


Figure 24. Dissolved oxygen (mg/l) at RM 19 in Dworshak Reservoir, 1972-74.

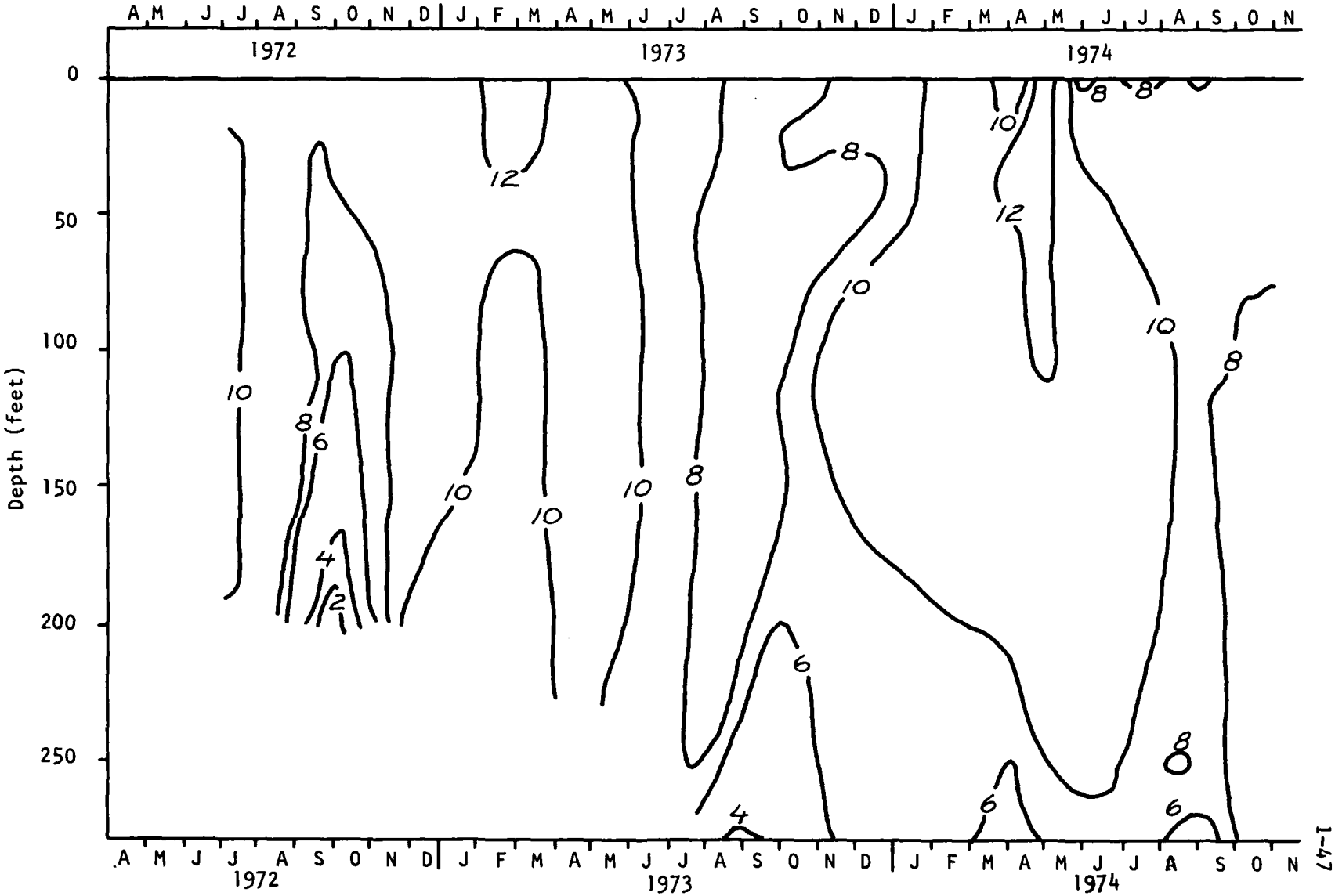


Figure 25. Dissolved oxygen (mg/l) at RM 35 in Dworshak Reservoir, 1972-74.

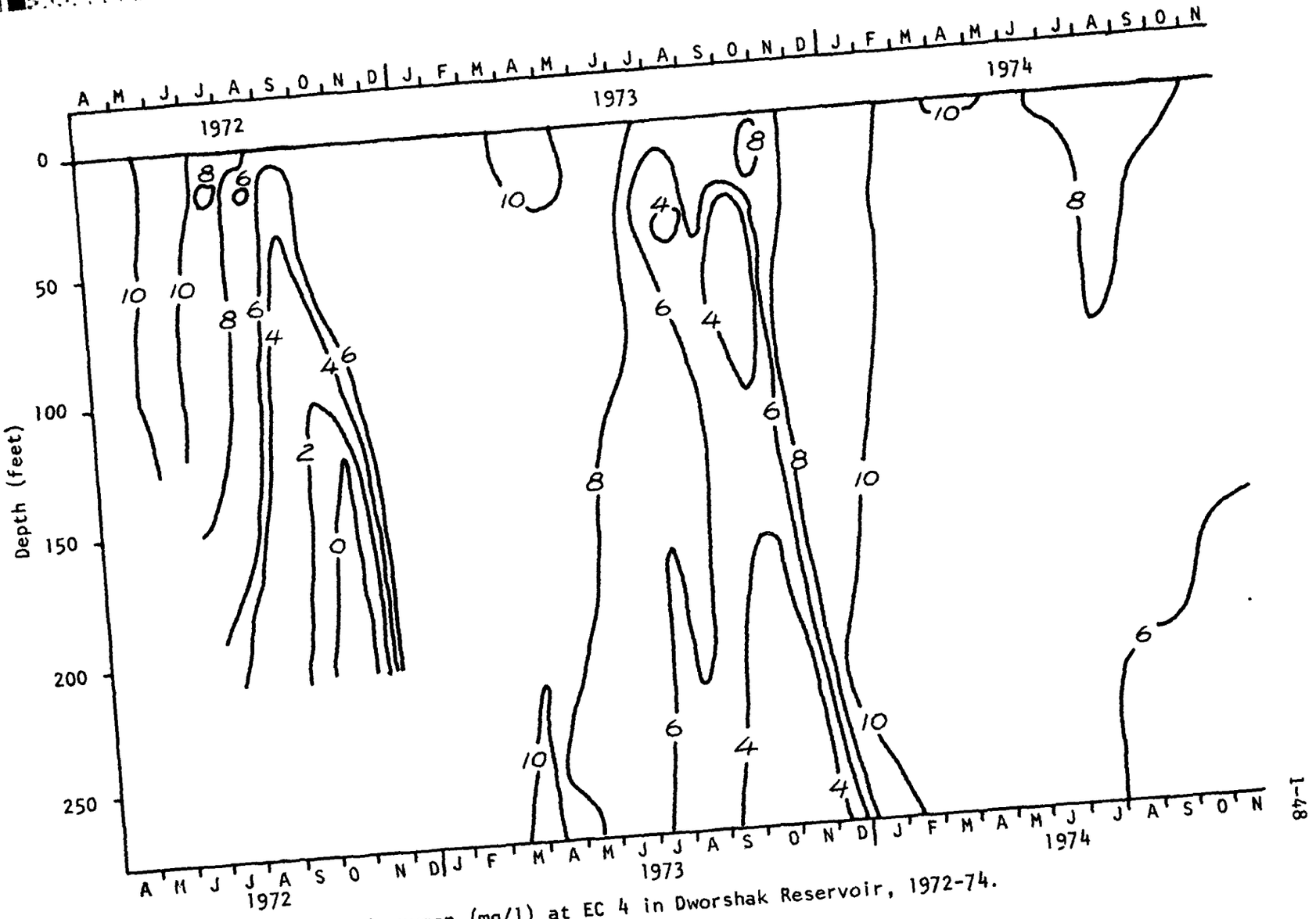


Figure 26. Dissolved oxygen (mg/l) at EC 4 in Dworshak Reservoir, 1972-74.

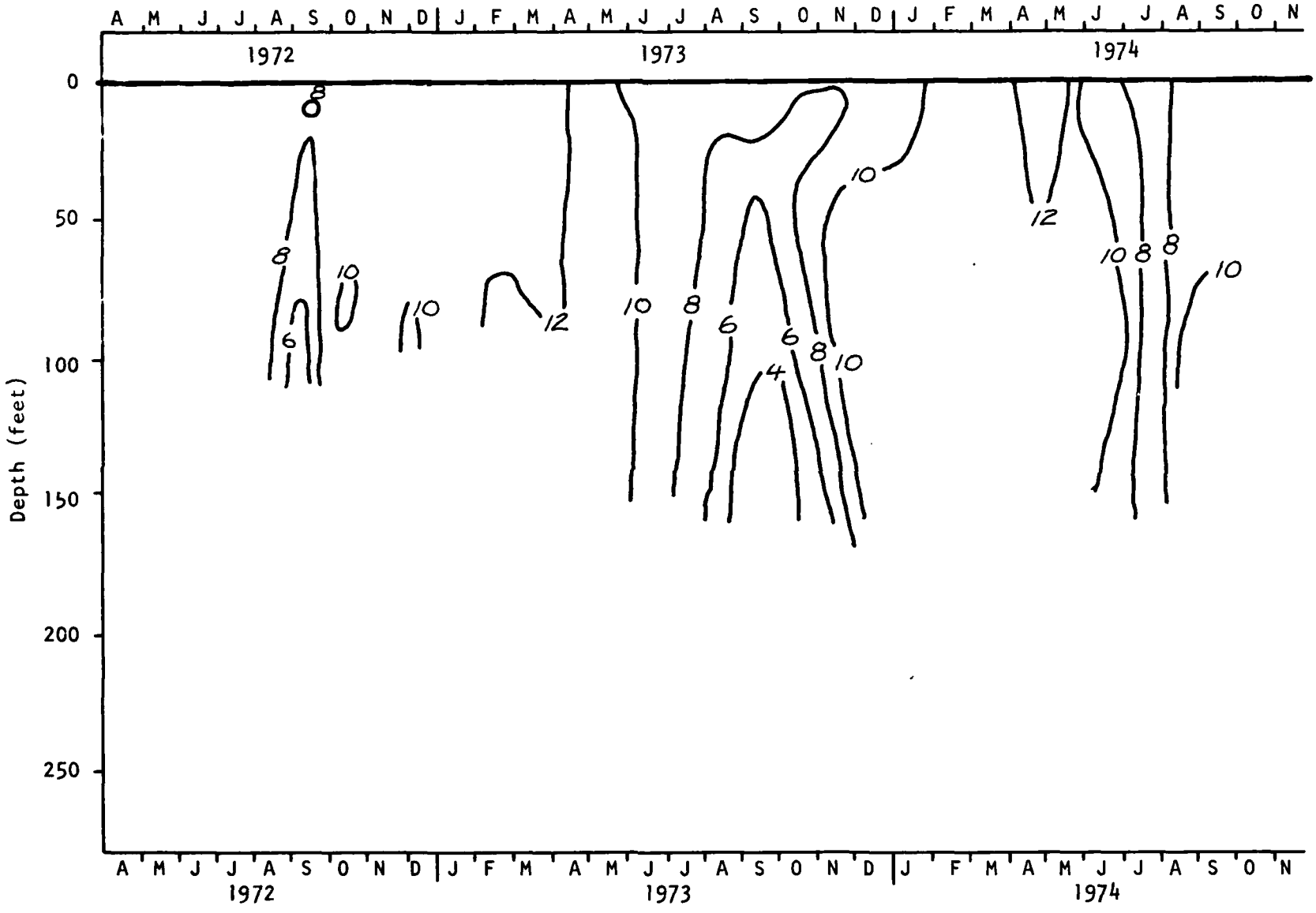


Figure 27. Dissolved oxygen (mg/l) at LNFK 1 in Dworshak Reservoir, 1972-74.

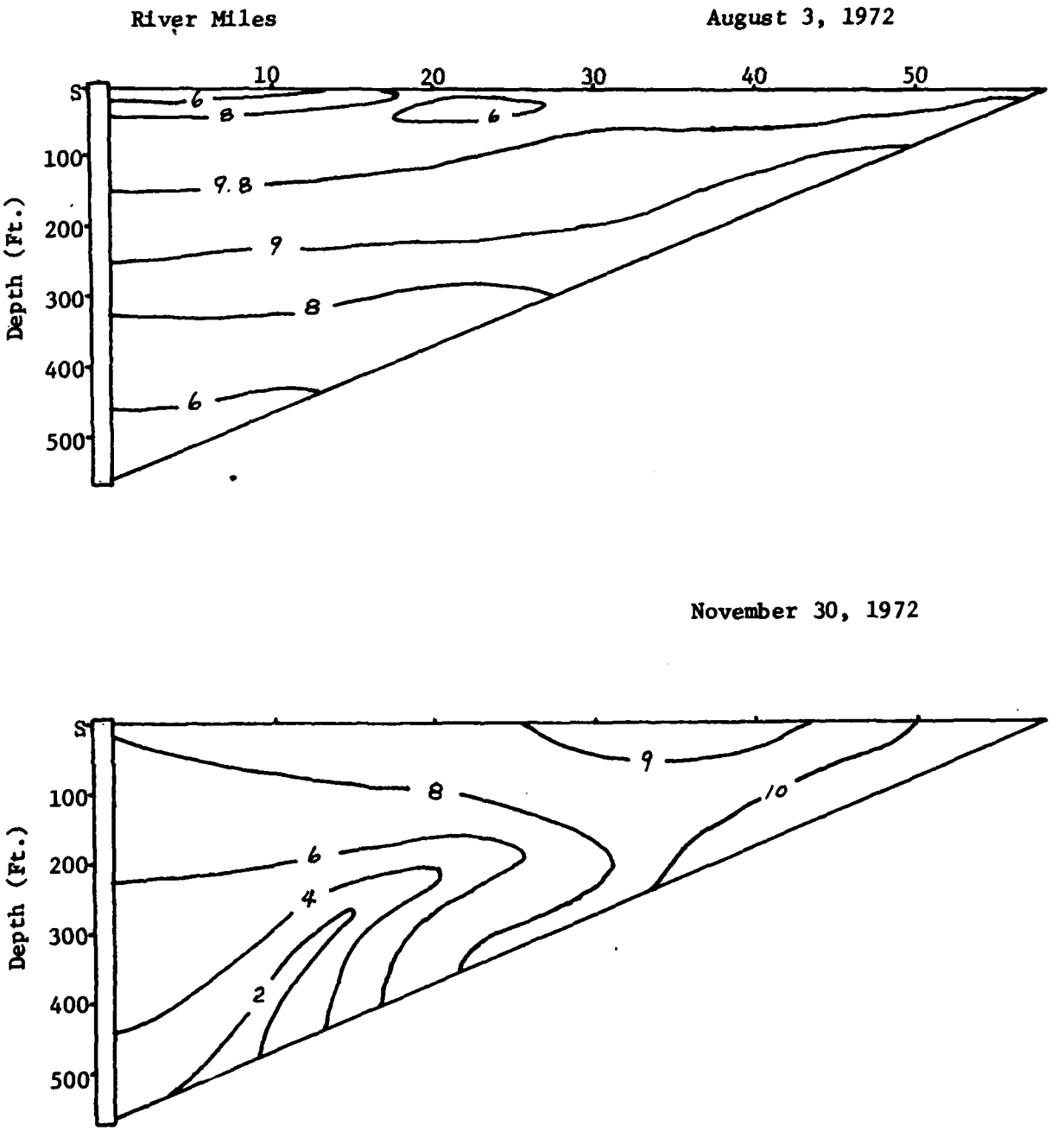


Figure 28. Longitudinal oxygen profiles (mg/ℓ) in Dworshak Reservoir, 1972.

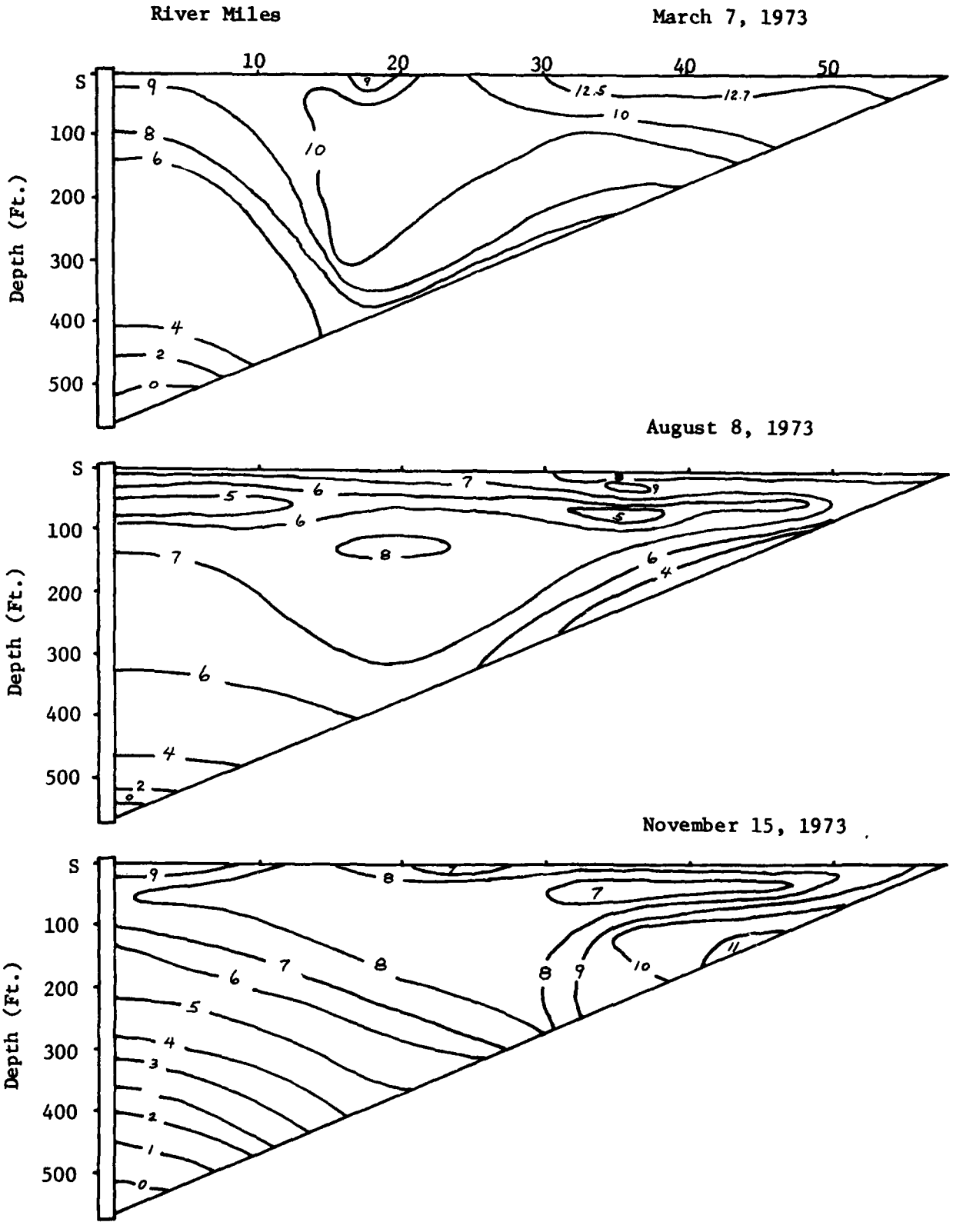


Figure 29. Longitudinal oxygen profiles (mg/ℓ) in Dworshak Reservoir, 1973.

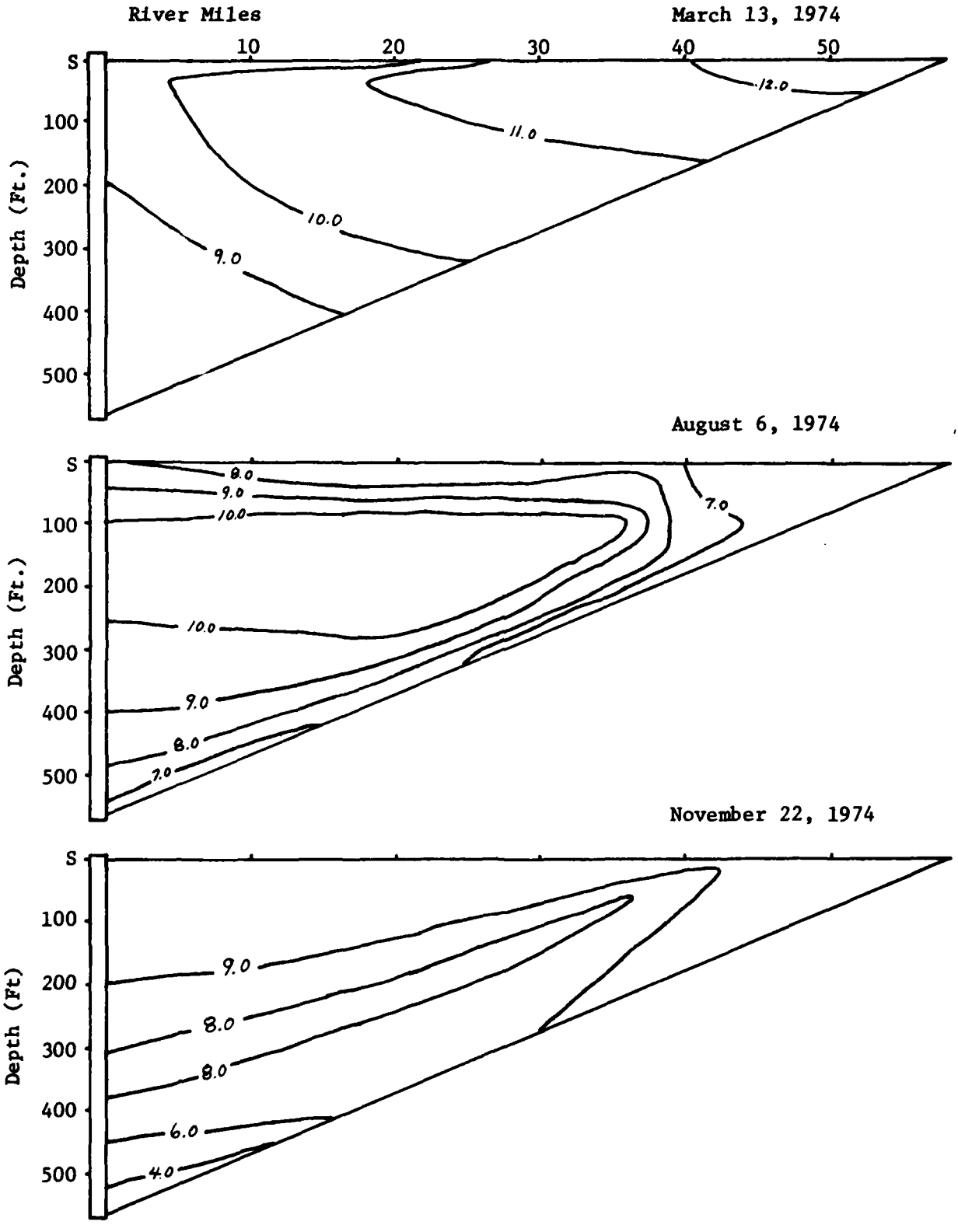


Figure 30. Longitudinal oxygen profiles (mg/ℓ) in Dworshak Reservoir, 1974.

Mean oxygen percent saturation of the deepwater layers at each reservoir station declined from a high of 68.2% at RM 19 to lows of 51.2% and 51.1% at RM 3 and EC 4 (Table 10). In 1972, EC 4 was the only site of low mean deepwater oxygen, but in 1973, RM 3 and RM 35 had low mean oxygen deepwater levels (29.6% and 31.0%). Oxygen deficits (mg O_2 consumed/cm^2 of hypolimnial surface/day from spring homothermy to maximum summer stratification) also followed this pattern, i.e., deepwater oxygen consumption was greatest at RM 35 in 1973 (Table 11). The 1973 deficit at RM 3 was very low because winter overturn and deepwater reoxygenation were only partial, resulting in a low spring to summer differential. At RM 19 oxygen consumption was lowest (3 year mean = 0.049). In 1974 very weak thermal stratification at RM 19 even resulted in a net increase of deepwater oxygen, thereby causing a positive oxygen deficit through the spring-summer period (Table 11).

Both oxygen percent saturation and hypolimnial oxygen deficits clearly reflect increasing oxygen levels in 1974. Yearly mean deficits were 0.101 mg/cm^2/day in 1972, 0.050 in 1973, and 0.038 in 1974. These mean oxygen deficits would normally offer a reasonable depiction of reservoir algae production in a stable lake but in these early years of Dworshak Reservoir oxygen levels were largely a function of allocthonous organic matter...that material contributed by newly submersed soils and vegetation. The log leaching work reported in Part 2 of this report indicates that readily available organic matter would be leached within the first two years, further supporting the conclusion that early low oxygen levels in Dworshak Reservoir were principally the result of allocthonous organic matter. The cold temperature of the hypolimnion slowed the rate of decomposition so that the low hypolimnetic O_2 conditions did not develop until early in 1973, more than a year after initiation of filling.

Table 10. Mean O_2 percent saturation of surface (S-40') and deep (below 100') layers of Dworshak Reservoir, 1972-74.

		1972	1973	1974	3-year mean
RM 3	Surf.	82.9	83.3	84.9	83.7
	Deep	64.4	29.6	59.6	51.2
RM 19	Surf.	91.4	77.1	83.7	84.0
	Deep	72.0	62.5	70.1	68.2
RM 35	Surf.	89.1	85.5	88.6	87.7
	Deep	69.1	31.0	66.7	55.6
EC 4	Surf.	85.0	74.2	82.2	80.4
	Deep	38.7	53.3	61.5	51.1
LNFK 1	Surf.	82.2	87.2	85.4	84.9
	Deep	--	57.1	69.3	63.2

Table 11. Summer hypolimnial O_2 deficits in Dworshak Reservoir, 1972-74 (from onset of stratification to maximal stratification in late summer).

	1972	1973	1974	3-year mean
RM 3	0.094	0.029	0.063	0.062
RM 19	0.124	0.046	+0.023	0.049
RM 35	0.084	0.082	0.058	0.075
EC 4	0.103	0.041	0.053	0.066
Reservoir Mean	0.101	0.050	0.038	0.063

Our oxygen deficit data indicate that Dworshak was a eutrophic lake in the first year but tended towards mesotrophy in 1973 and 1974. Wetzel (1975) gives 0.05 mg $O_2/cm^2/day$ as an oxygen consumption rate as on the upper limit of mesotrophy, but he cautions against sole reliance on oxygen deficits in deep lakes. The relation of oxygen deficits with autocthonous productivity diminishes both with increasing depth and import of allocthonous organic matter. The high oxygen consumption rates in Dworshak Reservoir (0.029 to 0.124 mg $O_2/cm^2/day$) reflect these concerns (Table 11). Downstream oxygen concentrations were adequate even in 1973, the year of minimal oxygen in deep waters of the reservoir.

Hydrogen Sulfide

Hydrogen sulfide was detected in concentrations up to 0.002 mg/1 only at RM 3 in 1973 and then only below 540 ft. It can only occur in the absence of O_2 since H_2S is spontaneously oxidized so it would be expected only at those times and locations of 0 O_2. Hydrogen sulfide was never analytically detected at EC 4, the one other location of 0 O_2, but sampling teams did observe an H_2S smell from near bottom samples at EC 4 when O_2 was 0. Hydrogen sulfide was never detected downstream of the dam.

Water Chemistry

Chemical composition of the North Fork of the Clearwater River is determined primarily by surface parent material of the drainage...a decomposed granite of the Idaho Batholith. Water flowing from a watershed in the Idaho Batholith is characterized by high inorganic suspended load, low dissolved ion content, and generally low levels of plant

nutrients.

Waters of a new reservoir are expected to be rich in nutrients because of their solution from newly submerged soils and vegetation. Dworshak Reservoir obtained a yet higher nutrient loading from submergence of a large amount of standing brush and timber and from the flotation of more than 30 million board feet of saw timber and associated slash on the reservoir for up to 18 months before removal. The result was a level of dissolved nutrients high enough to sustain intermittent algal blooms in water not expected to contain heavy algal growths.

Conductivity in 1971-74 averaged only 28 µmho and bicarbonate alkalinity 14 mg l^{-1}. Conductivity, as a measure of all ions in solution, is a convenient index of gross water quality trends over time. Conductivity declined from 1972 through 1974, as shown by conductivity decreasing from ~28 µmhos in 1972 to ~20 µmhos in 1974 in the 0-40 ft layer at RM 3 (Figure 31). Trends were erratic within a year as organic production and subsequent decomposition controlled ionic concentrations, but the overall trend is down. Deep lakes or reservoirs with near surface discharges typically act as ion traps, with a net retention of ions as water passes through them. The nutrient trap phenomenon is also seen in a comparison of conductivity between upper and lower reservoir sites in 1974 where the upper reservoir average surface conductivity through the year was 31.7 µmhos compared to 21.3 µmhos in the lower reservoir.

Future years should see a continuation of this trend, with lower reservoir surface conductivity stabilizing at 15-20 µmhos.

Dissolved ion load always increased with depth in the lower reservoir as sinking of organic matter into the hypolimnion and its subsequent decomposition resulted in conductivities as high as 95 µmhos at 540 ft.

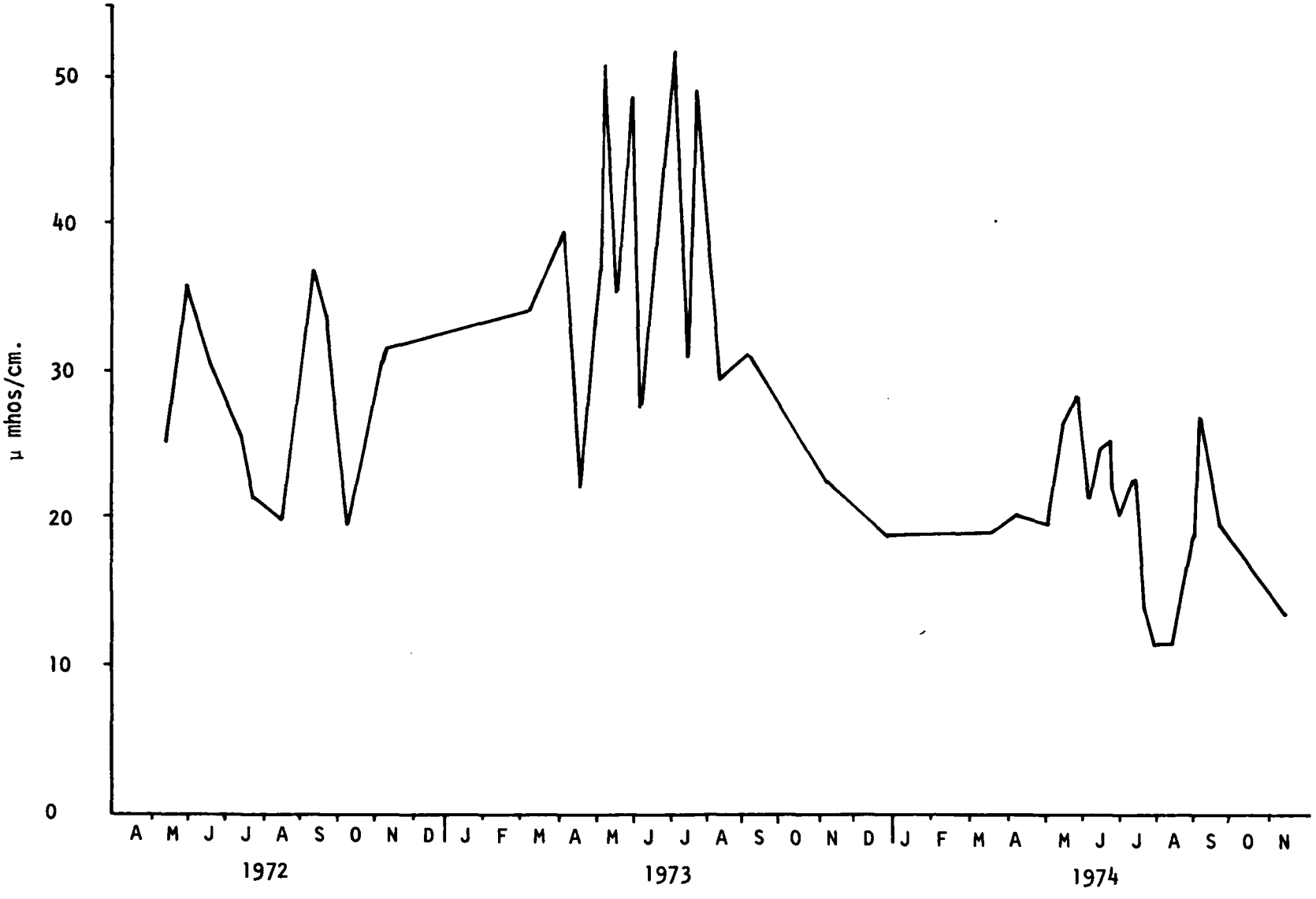


Figure 31. Conductivity (µ mhos/cm) at RM 3 in the 0-40 foot layer of Dworshak Reservoir, 1972-1974.

Upper reservoir sites also showed increased conductivity with depth but underflows from tributaries sometimes resulted in lower conductivities immediately off bottom at LNFK 1 and over at RM 35, 20 miles into the reservoir.

Over the study, nitrate nitrogen averaged .029 mg/1, orthophosphorous .015 mg/1, and total phosphorous .028 mg/1. These ions were initially high in 1972, near minimum detection limits through the 1973 growing season, and sporadically higher in 1974 (Figure 32). Mean nitrate and orthophosphate concentrations in the 0-40 ft layer of all stations showed similar 1973 lows (Table 12). Average N and P concentrations within a year were similar between sites (Table 12); the more productive sites simply showed more variability in response to nutrient uptake and release. Similar trends were also shown by iron, silica, bicarbonate, and sulfate, i.e. low in 1973.

Nitrogen and phosphorous concentrations suggest a superabundance of P in 1972 except in September when limnetic bacterial populations apparently tied up all available P. Nitrogen rose and fell inversely with algal biomass from near 0 in the new reservoir to .09 mg/1 following a mid-summer Anabaena bloom and to .12 mg/1 over the 1972-73 winter.

Nitrogen:phosphorous ratios (soluble forms) also suggest a superabundance of P...at least in 1972 and 1973 since N:P ratios did not exceed 6.30. The pool of inorganic N developed from near 0 in 1972 to ~0.3 mg/1 in 1974.

Trace element concentrations were consistently very low (Table 13), illustrating two points:

1) Dworshak waters have low enough nutrient concentrations that trace element limitation is a strong possibility; and,

Table 12. Mean nitrate and ortho-phosphate concentrations (mg/l) in the 0-40 foot layer of Dworshak Reservoir, 1972-74.

		RM 3	RM 19	RM 35	EC 4	LNFK 1
				NO_3		
1972	Spring	-	-	-	-	-
	Summer-fall	0.052	0.032	0.031	0.045	0.031
1973	Spring	0.021	0.039	0.029	0.026	0.033
	Summer-fall	0.015	0.019	0.018	0.017	0.017
1974	Spring	0.064	0.056	0.049	0.030	0.063
	Summer-fall	0.046	0.041	0.045	0.036	0.045
				$O\text{-}PO_4$		
1972	Spring	-	-	-	-	-
	Summer-fall	0.019	0.010	0.012	0.022	0.027
1973	Spring	0.014	0.016	0.010	0.015	0.010
	Summer-fall	0.011	0.011	0.010	0.012	0.011
1974	Spring	0.011	0.010	0.010	0.010	0.010
	Summer-fall	0.017	0.017	0.016	0.019	0.015

Table 13. Trace metals concentrations (mg/ℓ) at RM 3 in Dworshak Reservoir, 1972-74.

Date	Depth (ft.)	Ca	Cd	Cu	Fe	Hg	Mg	Mn	Mo	Na	Pb	Zn
July 7, 1972	0	1.8	<0.02	<0.05	0.10	.007	0.6	<0.1	<0.5	1.5	<0.10	<0.05
	10	1.8	<0.02	<0.05	<0.10	.007	0.6	<0.1	<0.5	1.4	<0.10	<0.05
	20	1.9	<0.02	<0.05	<0.10	.003	0.6	<0.1	<0.5	1.5	<0.10	<0.05
	40	1.6	<0.02	<0.05	<0.10	.004	0.4	<0.1	<0.5	1.0	<0.10	<0.05
	150	1.3	<0.02	<0.05	<0.10	.003	0.4	<0.1	<0.5	0.9	<0.10	<0.05
November 2, 1972	0	2.4	<0.02	<0.05	<0.10	<.001	0.6	<0.1	<0.5	1.3	<0.10	<0.05
	80	1.3	<0.02	<0.05	<0.10	.005	0.3	<0.1	<0.5	0.5	<0.10	<0.05
	530	3.0	<0.02	<0.05	<0.10	.003	1.0	0.2	<0.5	1.8	<0.10	<0.05
November 29, 1972	0	2.2	<0.02	<0.05	<0.10	>.008	0.6	<0.1	<0.5	1.2	<0.10	<0.05
	40	2.4	<0.02	<0.05	<0.10	>.008	0.6	0.1	<0.5	1.3	<0.10	<0.05
	530	2.6	<0.02	<0.05	<0.10	>.008	1.0	<0.1	<0.5	1.8	<0.10	<0.05
March 7, 1973	0	2.4	<0.02	<0.05	<0.10	>.008	0.7	0.1	<0.5	1.3	<0.10	<0.05
	540	4.1	<0.02	<0.05	<0.10	>.008	1.4	1.4	<0.5	1.8	<0.10	<0.05
April 4, 1973	0	2.6	<0.02	<0.05	<0.10	>.008	0.7	<0.1	<0.5	1.3	<0.10	<0.05
	540	3.4	<0.02	<0.05	<0.10	>.008	1.0	0.6	<0.5	1.6	<0.10	<0.05
June 7, 1973	0	2.8	<0.02	<0.05	<0.10	<.001	0.8	<0.1	<0.5	1.4	<0.10	<0.05
	40	2.8	<0.02	<0.05	<0.10	.001	0.8	<0.1	<0.5	1.4	<0.10	<0.05
	580	3.5	<0.02	<0.05	<0.10	.002	1.0	0.4	<0.5	1.5	<0.10	<0.05
June 14, 1973	0	3.0	<0.02	<0.05	<0.10	>.008	0.8	<0.1	<0.5	1.6	<0.10	<0.05
	600	3.8	<0.02	<0.05	<0.10	<.001	1.2	0.3	<0.5	1.7	<0.10	<0.05
July 12, 1973	0	3.0	<0.02	<0.05	<0.10	>.008	0.8	<0.1	<0.5	1.6	<0.10	<0.05
	150	2.6	<0.02	<0.05	<0.10	>.008	0.8	<0.1	<0.5	1.6	<0.10	<0.05
	600	3.6	<0.02	<0.05	<0.10	>.008	1.1	1.0	<0.5	1.7	<0.10	<0.05
July 19, 1973	0	3.1	<0.02	<0.05	<0.10	.002	0.9	<0.1	<0.5	1.6	<0.10	<0.05
	600	3.8	<0.02	<0.05	<0.10	>.008	1.2	1.2	<0.5	1.8	<0.10	<0.05
July 26, 1973	0	3.1	<0.02	<0.05	<0.10	>.008	1.0	<0.1	<0.5	1.6	<0.10	<0.05
	595	3.0	<0.02	<0.05	<0.10	>.008	1.0	0.1	<0.5	1.7	<0.10	<0.05
August 9, 1973	0	4.2	<0.02	<0.05	<0.10	.002	0.9	<0.1	<0.5	1.6	<0.10	<0.05
	590	3.5	<0.02	<0.05	<0.10	.004	1.1	0.8	<0.5	1.6	<0.10	<0.05
August 16, 1973	0	3.3	<0.02	<0.05	<0.10	<.001	0.8	<0.1	<0.5	1.6	<0.10	<0.05
	610	3.5	<0.02	<0.05	<0.10	<.001	1.0	0.6	<0.5	1.7	<0.10	<0.05
September 6, 1973	0	2.8	<0.02	<0.05	<0.10	>.008	0.9	<0.1	<0.5	1.6	<0.10	<0.05
	580	4.0	<0.02	<0.05	<0.10	>.008	1.3	2.3	<0.5	1.0	<0.10	<0.05

Table 13. (Continued)

Date	Depth (ft.)	Ca	Cd	Cu	Fe	Hg	Mg	Mn	Mo	Na	Pb	Zn
October 4, 1973	0	3.0	0.02	0.05	<0.10	>.008	0.9	<0.1	<0.5	2.8	<0.10	<0.05
	550	3.2	0.02	0.05	0.70	>.008	1.1	0.9	<0.5	2.3	<0.10	<0.05
October 18, 1973	0	3.0	0.02	0.05	<0.10	>.008	0.90	<0.1	<0.5	1.8	<0.10	0.05
	560	4.2	-	0.05	2.20	>.008	1.20	3.0	-	1.9	<0.10	0.06
March 13, 1974	0	1.6	-	0.05	<0.10	<0.30	-	-	-		<0.10	0.05
	478	2.4	-	0.05	<0.10	<0.30	-	-	-	3.0	<0.10	0.20
May 22, 1974	0	2.6	-	0.05	0.50	<0.30	0.75	-	-	2.7	<0.10	0.10
	500		-	0.05	0.83	<0.30	-	-	-		<0.10	<0.05
May 28, 1974	0	1.7	-	0.05	<0.10	<0.30	0.70	-	-	1.9	<0.10	<0.05
	520	1.7	-	0.05	-	<0.30	0.70	-	-	2.1	<0.10	<0.05
June 13, 1974	0	1.3	-	0.05	<0.10	<0.30	0.65	-	-	1.8	<0.10	<0.05
	595	1.8	-	0.05	0.80	<0.30	0.75	-	-	2.0	<0.10	<0.05
June 17, 1974	0	1.1	-	0.05	<0.10	<0.30	0.45	-	-	1.9	<0.10	<0.40
	590	1.8	-	0.05	0.40	<0.30	0.80	-	-	1.9	<0.10	<0.05
June 25, 1974	0	1.2	-	0.05	<0.10	<0.30	0.55	-	-	1.7	<0.10	<0.05
	600	1.8	-	0.05	0.80	<0.30	0.70	-	-	1.9	<0.10	<0.05
July 2, 1974	0	.7	-	0.05	<0.10	<0.30	0.25	-	-	.5	<0.10	<0.05
July 11, 1974	0	.5	-	0.05	<0.10	<0.30	0.30	-	-	.5	<0.10	<0.05
	600	1.9	-	0.05	0.90	<0.30	0.85	-	-	1.9	<0.10	<0.05
July 16, 1974	0	1.2	-	0.05	<0.10	<0.30	0.50	-	-	1.5	<0.10	<0.05
	600	1.7	-	0.05	0.59	<0.30	0.75	-	-	1.7	<0.10	<0.05
July 23, 1974	0	1.2	-	0.05	<0.10	<0.30	0.50	-	-	1.5	<0.10	<0.05
	590	1.9	-	0.05	0.54	<0.30	0.90	-	-	1.3	<0.10	<0.05
July 30, 1974	0	1.3	-	0.05	<0.10	<0.30	0.50	-	-	1.8	<0.10	<0.05
	590	1.9	-	0.05	0.13	<0.30	0.90	-	-	1.8	<0.10	<0.05
August 6, 1974	0	1.3	-	0.05	<0.10	<0.30	0.55	-	-	1.4	<0.10	<0.05
	600	1.9	-	0.05	0.84	<0.30	0.95	-	-	1.8	<0.10	<0.05
August 19, 1974	0	1.3	-	0.05	<0.10	<0.30	0.50	-	-	1.4	<0.10	<0.05
	590	2.1	-	0.05	0.09	<0.30	0.80	-	-	1.8	<0.10	<0.05
August 27, 1974	0	1.4	-	0.05	<0.10	<0.30	0.55	-	-	1.4	<0.10	<0.05
	590	2.2	-	0.05	0.11	<0.30	0.85	-	-	1.9	<0.10	<0.05

Table 13. (Continued)

Date	Depth (ft.)	Ca	Cd	Cu	Fe	Hg	Mg	Mn	Mo	Na	Pb	Zn
September 5, 1974	0	1.5	-	0.05	<0.10	<0.30	0.60	-	-	1.3	<0.10	<0.05
	605	2.4	-	0.05	0.09	<0.30	0.95	-	-	1.9	<0.10	<0.05
October 3, 1974	0	1.6	-	0.05	< .10	<0.30	0.65	-	-	1.4	<0.10	<0.05
	580	2.3	-	0.05	0.06	<0.30	0.90	-	-	1.8	<0.10	<0.05
October 8, 1974	0	2.6	-	0.05	<0.10	<0.30	1.00	-	-	1.9	<0.10	<0.05
	590	1.7	-	0.05	<0.10	<0.30	0.60	-	-	1.3	<0.10	<0.05
October 29, 1974	0	1.6	-	0.05	<0.10	<0.30	0.55	-	-	1.3	<0.10	<0.05
	550	1.9	-	0.05	0.04	<0.30	0.75	-	-	1.9	<0.10	<0.05
November 22, 1974	0	1.1	-	0.05	<0.10	<0.30	0.60	-	-	1.2	<0.10	<0.05
	570	2.4	-	0.05	0.14	<0.30	0.95	-	-	1.8	<0.10	<0.05

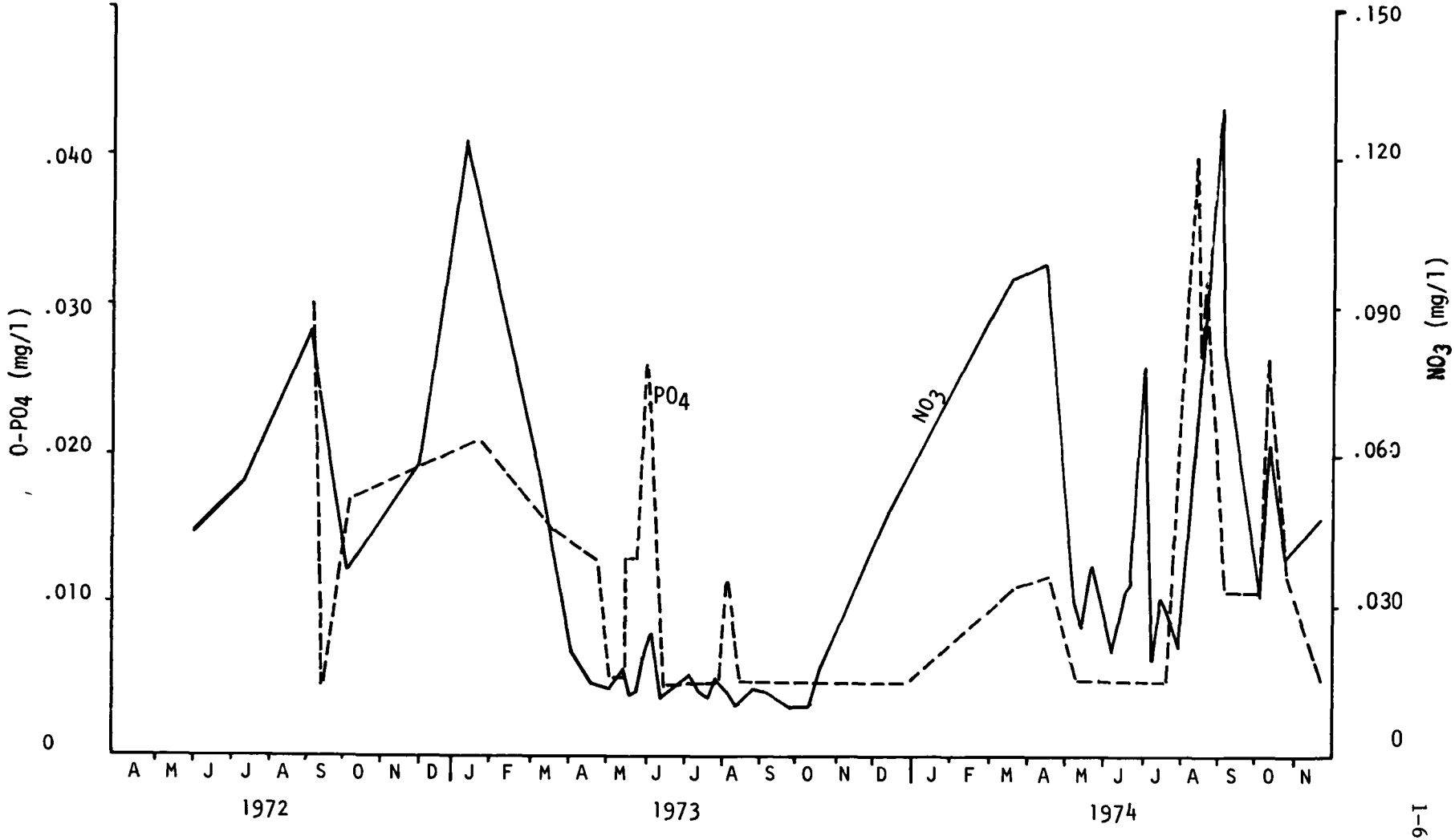


Figure 32. NO_3 and O-PO_4 concentration (mg/l) in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-74.

2) No potential toxicity from metals was indicated.

Phytoplankton

Mean total phytoplankton numbers in the 0-40 ft layer of Dworshak Reservoir are presented in Figures 33-37. Average summer-fall numbers of each major group by site are shown in Figure 38 and Table 14 while times and composition of major peaks are shown in Table 15.

During the first three years of impoundment, total algal numbers decreased from an average of 2.83×10^6 cells/l in 1972 to 3.44×10^5 cells/l in 1974. Green algae decreased more than other forms during these years. Bluegreens decreased from 1972 to 1973 and appeared to have stabilized by 1974. Diatoms remained relatively stable during the first years of impoundment. Up-reservoir stations exhibited more annual variation in average numbers of algae than downreservoir stations during the study. Therefore, the downreservoir stations are probably better indicators of future production trends.

In the spring of 1972, when the reservoir was filling, low numbers of coldwater diatoms of probable riverine origin were the only algal forms. Bluegreens appeared as a predominant summer form, and by fall, reservoir-type diatoms were in high numbers. Once diatoms were established in 1972, they became the predominant spring bloom form in 1973 and 1974. The occurrence of large spring concentrations of diatoms is common in deep water reservoirs and lakes and will likely continue to occur in Dworshak. Bluegreens, which bloomed in the summer of 1972 and 1973, were largely replaced by dinoflagellates in the summer of 1974. However, Aphanizomenon sp., a species not previously present in Dworshak, bloomed in late summer in 1974. Bluegreen production did not stabilize enough

Table 14. Overall means of phytoplankton cell numbers per liter in the 0-40 foot stratum of Dworshak Reservoir, 1972-1974.

		Entire Reservoir Mean	RM 3	RM-19	RM-35	EC-4	LNF-1
Total Algae	1972	28.3×10^5	40.8×10^5	18.9×10^5	20.2×10^5	28.0×10^5	22.4×10^5
	1973	11.1×10^5	15.2×10^5	7.87×10^5	14.6×10^5	7.65×10^5	0.38×10^5
	1974	3.44×10^5	5.24×10^5	1.12×10^5	1.56×10^5	3.58×10^5	1.47×10^5
Green Algae	1972	8.71×10^5	5.56×10^5	15.7×10^5	5.74×10^5	17.9×10^5	0.01×10^5
	1973	2.04×10^5	2.88×10^5	1.17×10^5	0.04×10^5	2.72×10^5	0.07×10^5
	1974	0.65×10^5	0.34×10^5	$0.1_{\text{illegible}} \times 10^5$	0.04×10^5	2.34×10^5	0.07×10^5
Blue-green	1972	14.10×10^5	34.6×10^5	0.05×10^5	4.41×10^5	0.07×10^5	10.4×10^5
	1973	1.54×10^5	1.16×10^5	1.45×10^5	5.56×10^5	0.42×10^5	0.0004×10^5
	1974	1.57×10^5	3.17×10^5	0.49×10^5	0.005×10^5	0.87×10^5	0.02×10^5
Diatoms	1972	5.39×10^5	0.68×10^5	3.23×10^5	9.78×10^5	10.0×10^5	11.6×10^5
	1973	7.46×10^5	11.1×10^5	6.30×10^5	7.06×10^5	4.41×10^5	0.30×10^5
	1974	1.02×10^5	1.47×10^5	0.38×10^5	1.45×10^5	0.26×10^5	1.01×10^5
Number of phytoplankton spp.	1972	3.76					
	1973	4.91					
	1974	5.46					

Table 15. Predominant phytoplankton genera comprising peaks in 1972-1974, RM 3 Dworshak Reservoir.

Date	Cell Numbers at Peak	Genera
July 19, 1972	$26.2 \times 10^6/\ell$	Anabaena
Oct. 6, 1972	7.6×10^6	Mougeotia Asterionella
April 4, 1973	6.7×10^6	Melosira Fragillaria-Asterionella
June 21, 1973	2.9×10^6	Mougeotia Fragillaria-Asterionella
July 26, 1973	$.9 \times 10^6$	Anabaena Fragillaria
Sept. 22, 1973	$.4 \times 10^6$	Staurastrum Fragillaria
May 9, 1974	1.0×10^6	Melosira Fragillaria
May 22, 1974	1.2×10^6	Melosira-Dinobryon
July 23-Aug. 14, 1974	10.4×10^6	Dinobryon
Oct. 3-Oct. 8, 1974	2.0×10^6	Aphanizomenon Anabaena

	SPRING	SUMMER	FALL
1972	——	blue-greens	diatoms
1973	diatoms	blue-greens	greens
1974	diatoms	dinoflagellates	blue-greens

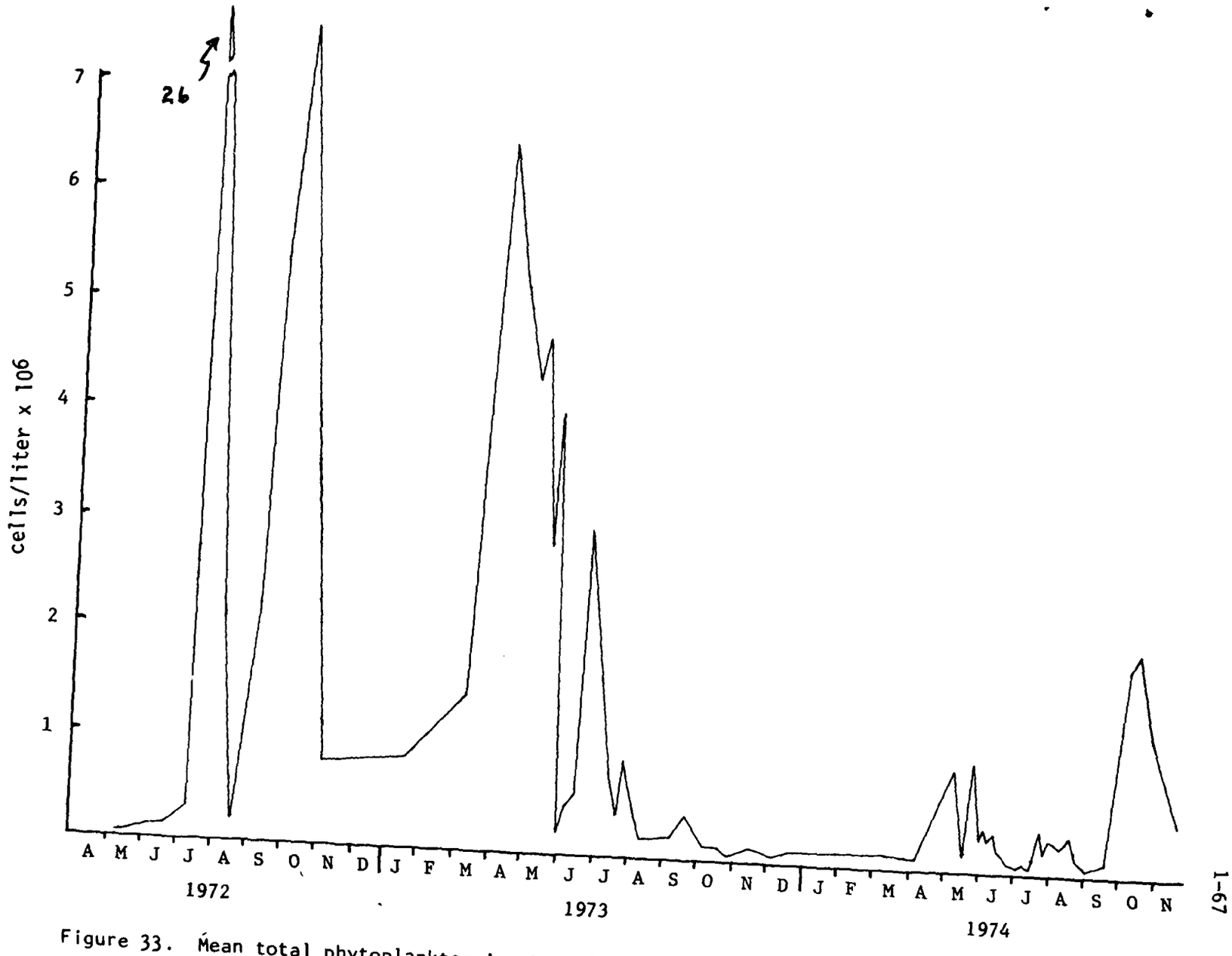


Figure 33. Mean total phytoplankton in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-74.

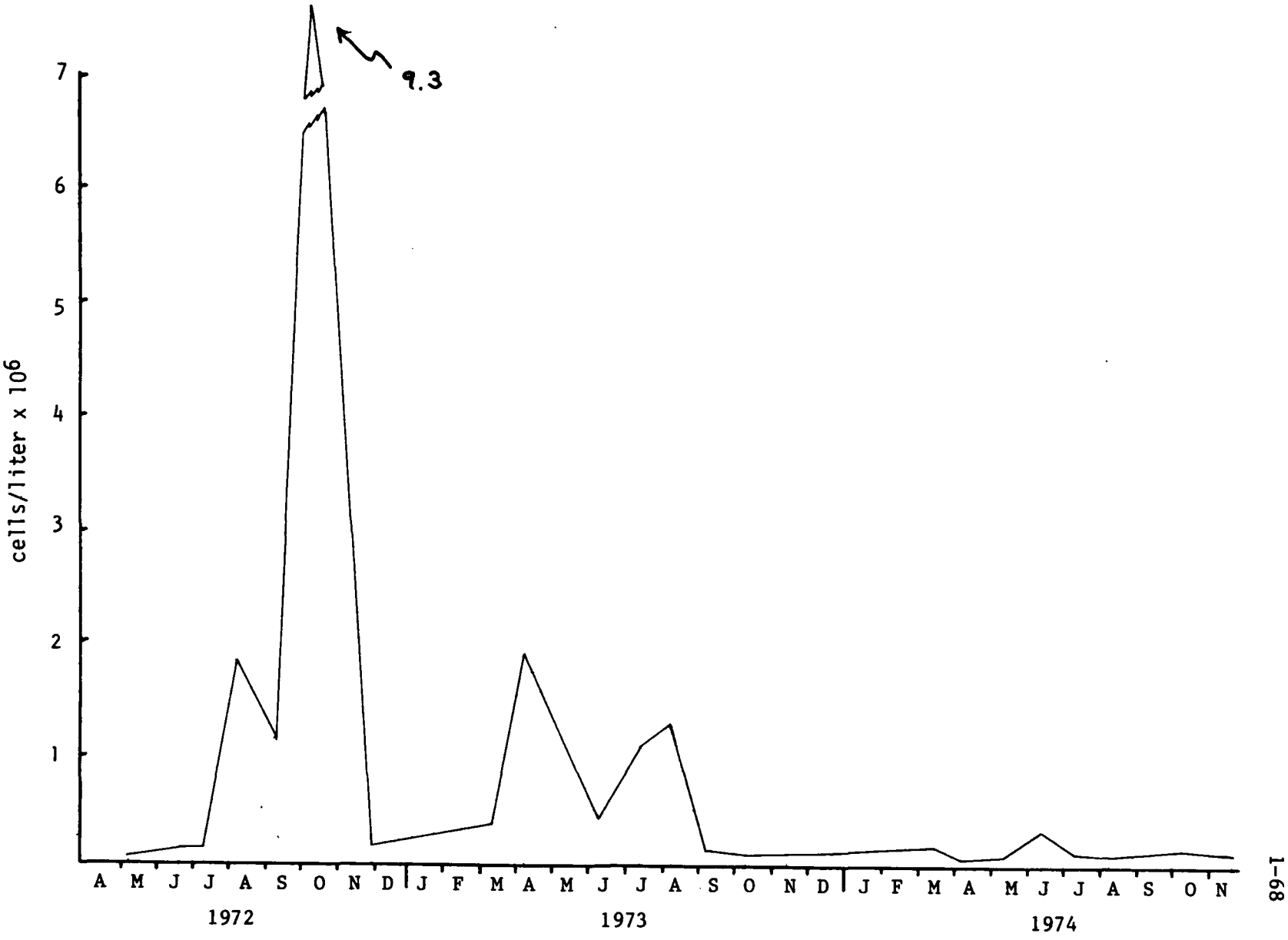


Figure 34. Mean total phytoplankton in the 0-40 foot layer at RM 19 in Dworshak Reservoir, 1972-74.

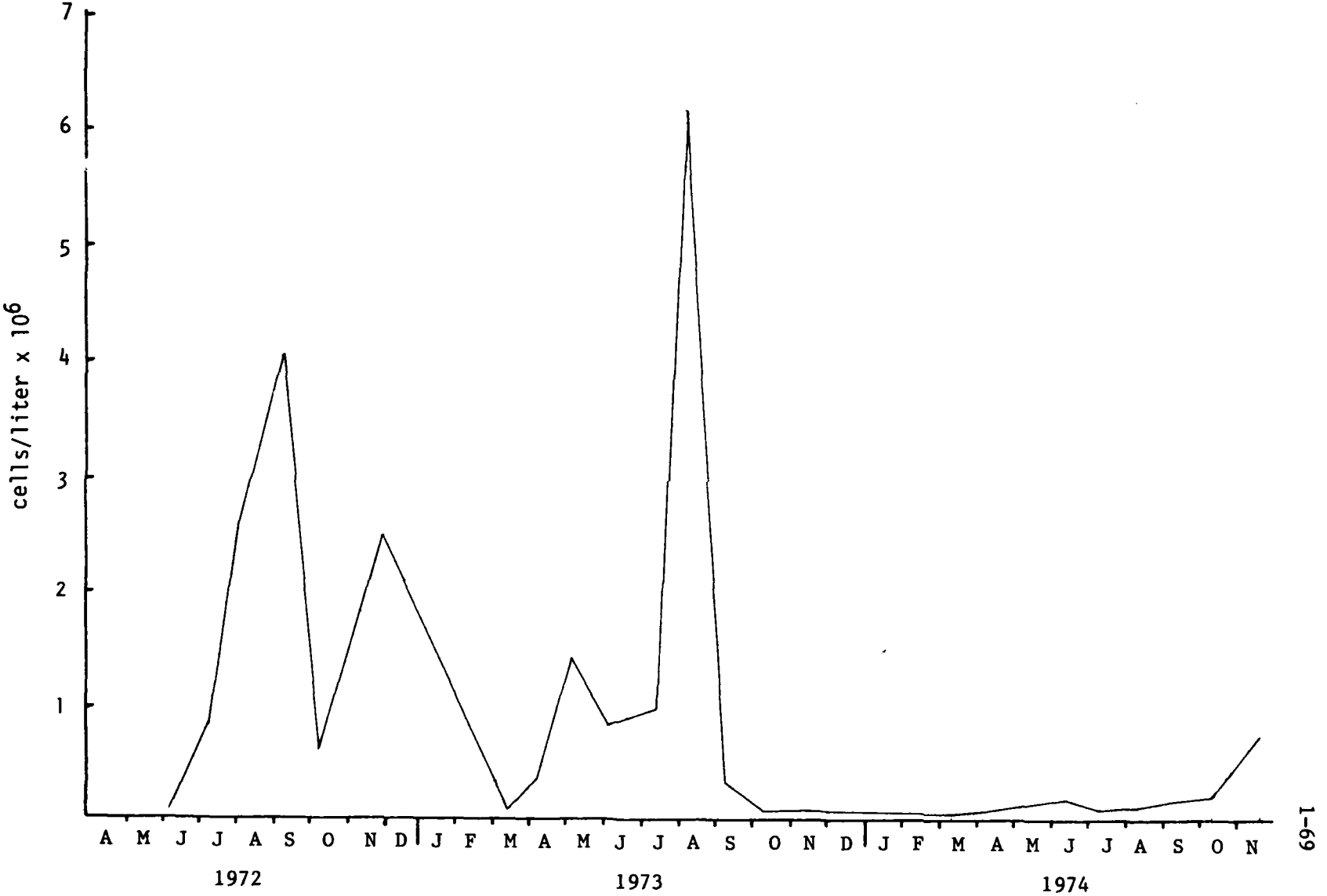


Figure 35. Mean total phytoplankton in the 0-40 foot layer at RM 35 in Dworshak Reservoir, 1972-74.

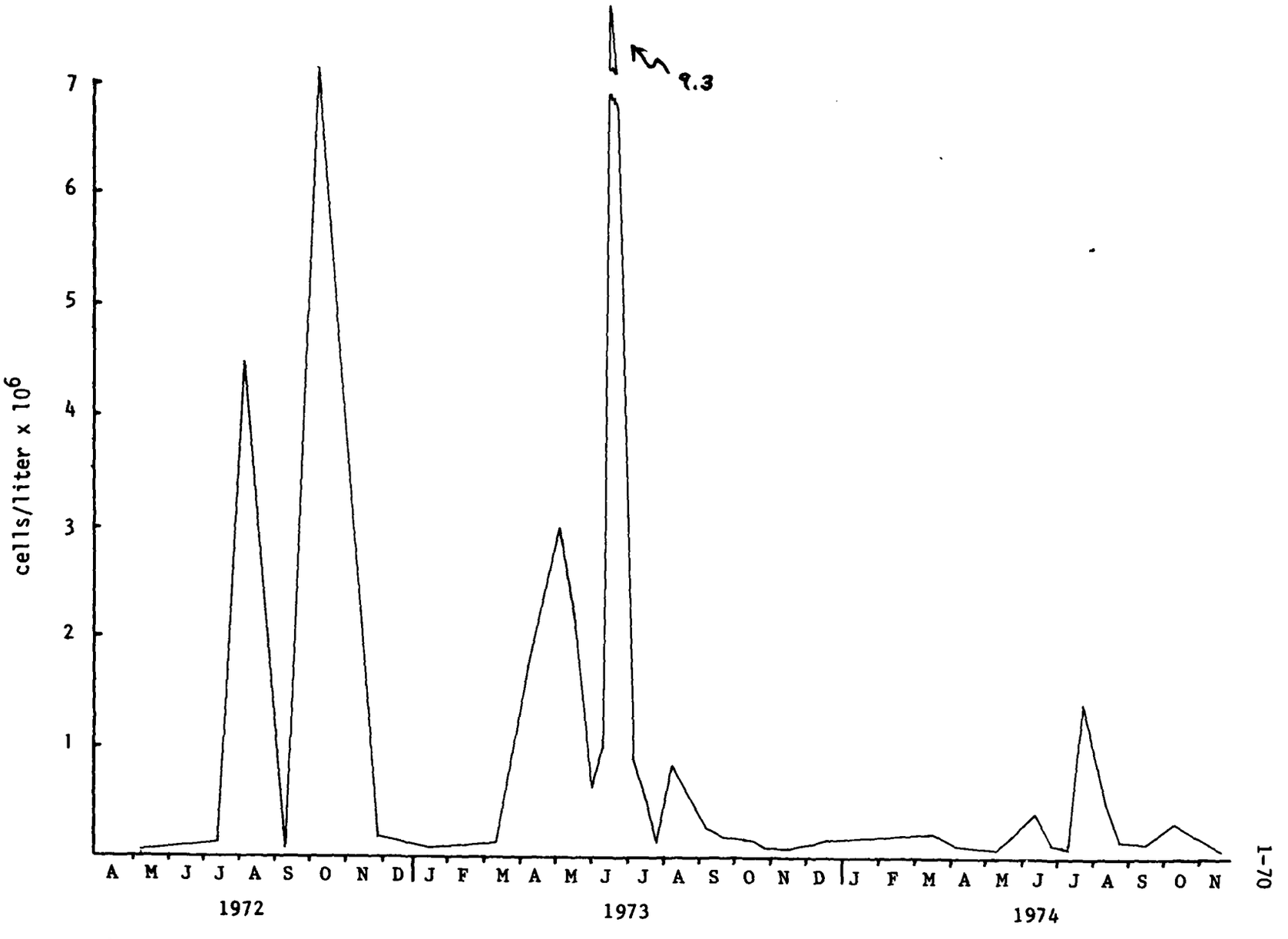


Figure 36. Mean total phytoplankton in the 0-40 foot layer at RM-EC 4 in Dworshak Reservoir, 1972-74.

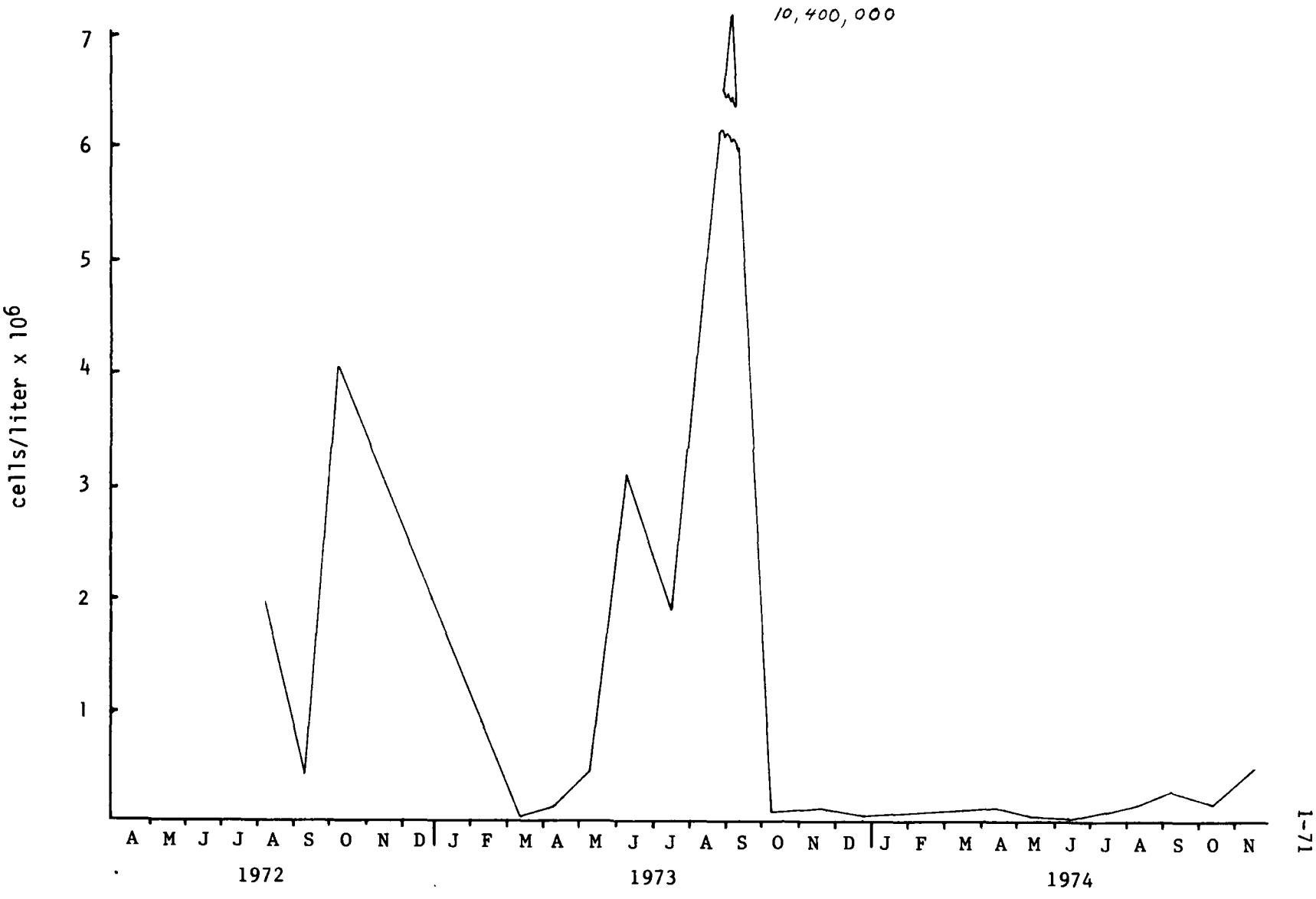


Figure 37. Mean total phytoplankton in the 0-40 foot layer at LNF-1 in Dworshak Reservoir, 1972-74.

during the three years to give any indication of future trends in numbers, species, or time of bloom. Maximum populations were attained in mid-July, 1972 with a pulse of Anabaena at 26.2 x 10^6 cells/1. Two weeks after the pulse, nitrate attained its highest concentration of the study before an extended mixed pulse of Mougeotia and Asterionella persisted for 8 weeks through the fall. Phytoplankton in 1973 was dominated by diatoms ~3 x 10^6 cells/1 with a brief mid summer Anabaena pulse (0.9 x 10^6 cells/1). The 1973 community was more stable with more persistent blooms and more genera per sample. Mean 1973 total numbers of algal cells were only 2 to 70% of 1972 mean numbers at five major stations (Table 14). Cell numbers at all stations exhibited similar trends between years even though composition and timing varied widely.

There was much less variation in total cell numbers between stations in 1974 when station means averaged 31.0% of 1973 individual station means but only 9.2% of 1972 means (Table 14). Melosira, Dinobryon, and Aphanizomenon dominated the 1974 spring, summer, and fall communities, respectively (Table 15).

Degree of eutrophy is reasonably expressed by summer-fall bluegreen algae numbers. Mean summer-fall bluegreen algae over all stations declined from 1.1 x 10^6 cells/1 in 1972 to .29 x 10^6 cells/1 in 1973 and .10 x 10^6 cells/1 in 1974. Three year means were highest at RM 3 (1.4 x 10^6 cells/1) while the other stations were .06 to .44 x 10^6 cells/1 (Table 16).

The average annual number of genera of algae per sample in the reservoir increased from 3.76 in 1972 to 4.91 in 1973 and was 5.46 in 1974. This increase in number of species, along with a decrease in cell concen-

Table 16. Summer-fall average bluegreen algae (cells/liter) in Dworshak Reservoir 0-40' layer, 1972-74.

	1972	1973	1974	3-year mean
RM 3	3.89×10^6	$.16 \times 10^6$	$.27 \times 10^6$	1.44×10^6
RM 19	$.01 \times 10^6$	$.23 \times 10^6$	$.08 \times 10^6$	$.11 \times 10^6$
RM 35	$.70 \times 10^6$	$.60 \times 10^6$	$.02 \times 10^6$	$.44 \times 10^6$
EC 4	$.01 \times 10^6$	$.07 \times 10^6$	$.10 \times 10^6$	$.06 \times 10^6$
LNFK 1	$.63 \times 10^6$	$.39 \times 10^6$	$.01 \times 10^6$	$.32 \times 10^6$
All Stations Combined	1.05×10^6	$.29 \times 10^6$	$.10 \times 10^6$	

tration, indicates that the reservoir is approaching a lower production level. Also, total algal production became less variable throughout the reservoir in the third year of impoundment.

Carbon-14 productivity estimates conducted in 1973 and 1974 support this trend of declining production from 1972 to 1974. Total epilimnial (0-40 ft) algal production in 1974 was only 27.9% of 1973 production, the decline agreeing closely with peaks and lows in total cell numbers (Figures 39 and 40). Summer-fall epilimnial algal production averaged 9.1 mg $C^{12}/m^3/hr$ in 1973 but only 3.6 mg $C^{12}/m^3/hr$ in 1974. EC 4, the carbon-14 site representative of tributary arms experienced similar productivity declines in 1974.

Zooplankton

Summer-fall (June-October) zooplankton peaked in 1972 in the lower reservoir (Figures 41 and 42). Maximum daily peak was 99,600 individuals/m^3 on July 19, 1972, at the maximum observed Anabaena peak. Early dominant forms were Bosmina and Ceriodaphnia (Table 18). Overall reservoir mean concentrations of zooplankton were 27,300/m^3 in 1972, 18,500/m^3 in 1973, and 10,800/m^3 in 1974. Numbers ranged from 55,000 to 105,000 individuals/m^3, approximately 50% cladocerans. The decline in numbers through 1974 is striking; 1974 populations were 7-49% 1972 numbers (Table 17). In 1974, lower reservoir sites still contained a relatively even mix of cladocerans and copepods but the upper reservoir composition was predominantly cladocerans (Figure 46). RM 3 and EC 4 in the lower reservoir zooplankton generally exceeded upper reservoir zooplankton numbers.

As with phytoplankton, the peak concentrations were smaller in 1974 than in 1972. However, zooplankton peaks became more numerous and there

Table 17 Overall means of zooplankton numbers per cubic meter in the 0-33 foot stratum of Dworshak Reservoir, 1972-1974.

		Entire Reservoir Mean	RM 3	RM-19	RM-35	EC-4	LNF-1
Total Zooplankton	1972	2.73×10^4	8.57×10^4	3.86×10^4	1.71×10^4	3.27×10^4	1.91×10^4
	1973	1.85×10^4	2.26×10^4	1.02×10^4	1.35×10^4	2.59×10^4	0.58×10^4
	1974	1.08×10^4	1.12×10^4	0.21×10^4	0.32×10^4	1.68×10^4	0.16×10^4
Cladocerans	1972	2.52×10^4	2.65×10^4	3.52×10^4	1.66×10^4	3.09×10^4	1.86×10^4
	1973	1.04×10^4	1.34×10^4	0.43×10^4	0.69×10^4	1.43×10^4	0.41×10^4
	1974	0.91×10^4	1.00×10^4	0.18×10^4	0.22×10^4	1.35×10^4	0.12×10^4
Total Copepods	1972	0.21×10^4	5.92×10^4	0.34×10^4	0.05×10^4	0.18×10^4	0.05×10^4
	1973	0.81×10^4	0.92×10^4	0.58×10^4	0.66×10^4	1.16×10^4	0.17×10^4
	1974	0.17×10^4	0.12×10^4	0.03×10^4	0.10×10^4	0.33×10^4	0.04×10^4
Cladocerans as % of total zooplankton	1972	92.3%	30.9%	91.2%	97.1%	94.5%	97.4%
	1973	56.2%	59.3%	42.2%	51.1%	55.2%	70.7%
	1974	84.3%	89.3%	85.7%	68.8%	80.4%	75.0%
Mean number of zooplankton species per sample:	1972	4.79					
	1973	3.65					
	1974	3.67					

Table 18. Predominant zooplankton genera comprising peaks at RM 3 in Dworshak Reservoir, 1972-1974.

Date	Numbers at Peak (per m^3)	Genera
July 19, 1972	9.96×10^4	Bosmina Ceriodaphnia
Oct. 3, 1972	1.49×10^4	Ceriodaphnia Daphnia
April 22, 1973	3.53×10^4	Copepods Bosmina
May 24, 1973	6.00×10^4	Daphnia Copepods
July 12, 1973	4.22×10^4	Copepods Daphnia
Aug. 30, 1973	4.34×10^4	Bosmina Daphnia-Copepods
Oct. 28, 1973	4.49×10^4	Bosmina Copepods
May 4, 1974	0.30×10^4	Bosmina Daphnia
June 25, 1974	1.29×10^4	Copepods Daphnia
July 9, 1974	3.70×10^4	Daphnia Copepods-Bosmina
July 30, 1974	2.35×10^4	Polyphemus Bosmina-Daphnia
Aug. 19, 1974	2.94×10^4	Daphnia Bosmina-Holopedium
Sept. 20-Oct. 3, 1974	1.30×10^4	Ceriodaphnia Bosmina-Daphnia

	SPRING	SUMMER	FALL
1972	—	Bosmina	Ceriodaphnia
1973	Copepods (Daphnia)	Bosmina	Bosmina
1974	Bosmina	Copepods Daphnia Polyphemus	Daphnia-Ceriodaphnia

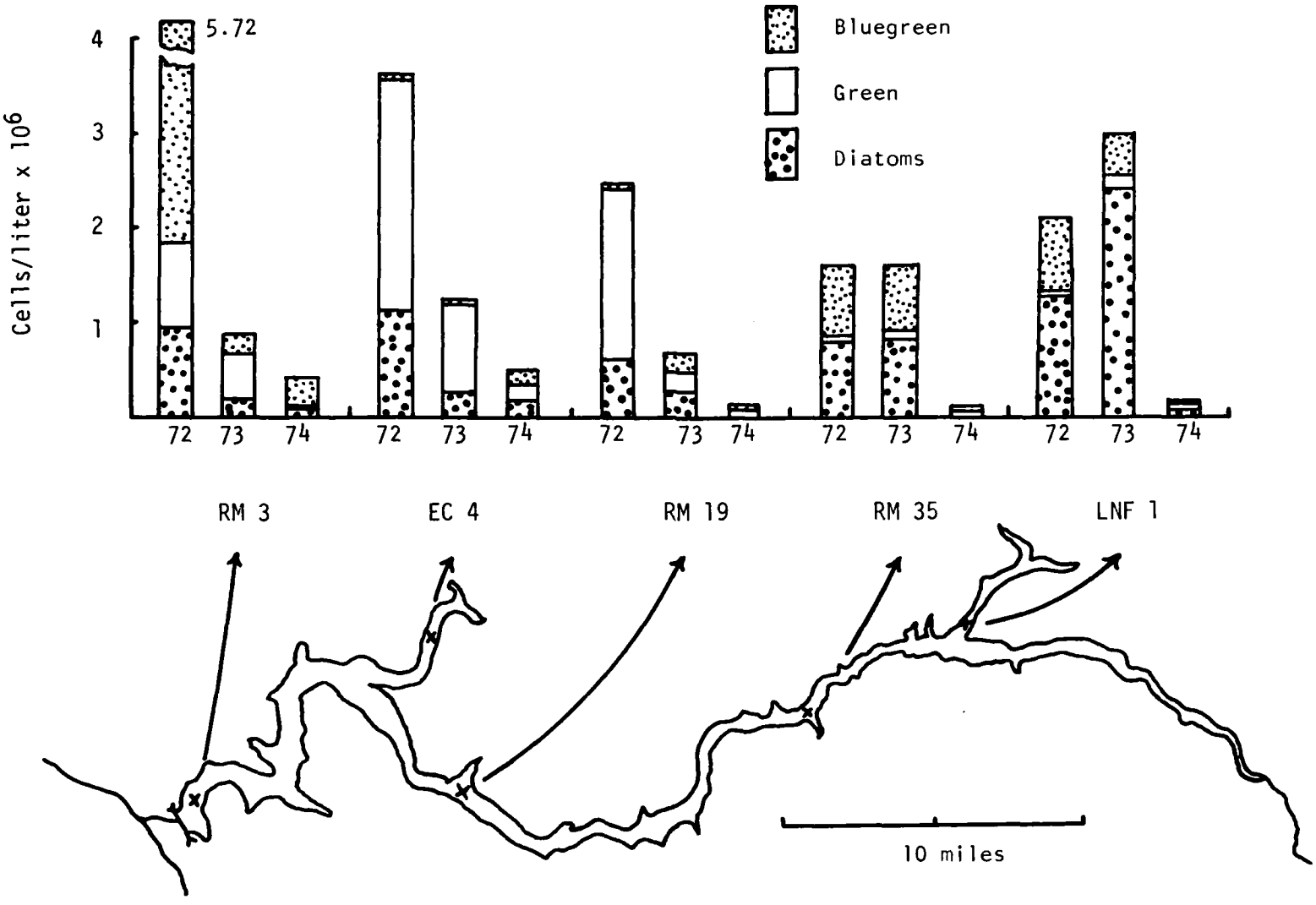


Figure 38. Average summer-fall (June-October) algae numbers in the 0-40 foot layer of Dworshak Reservoir, 1972-1974.

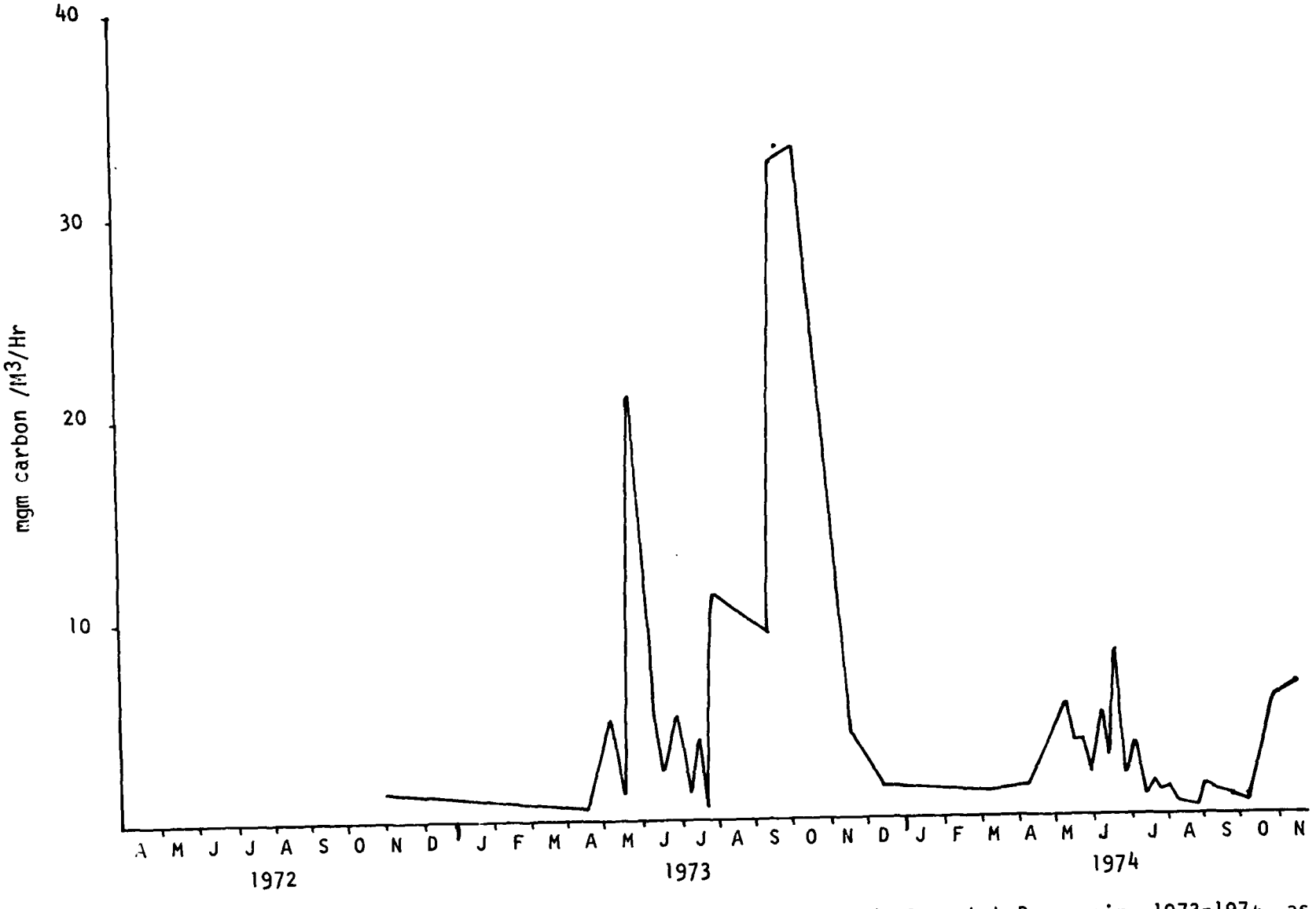


Figure 39. Mean carbon uptake in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1973-1974, as measured by the carbon-14 method.

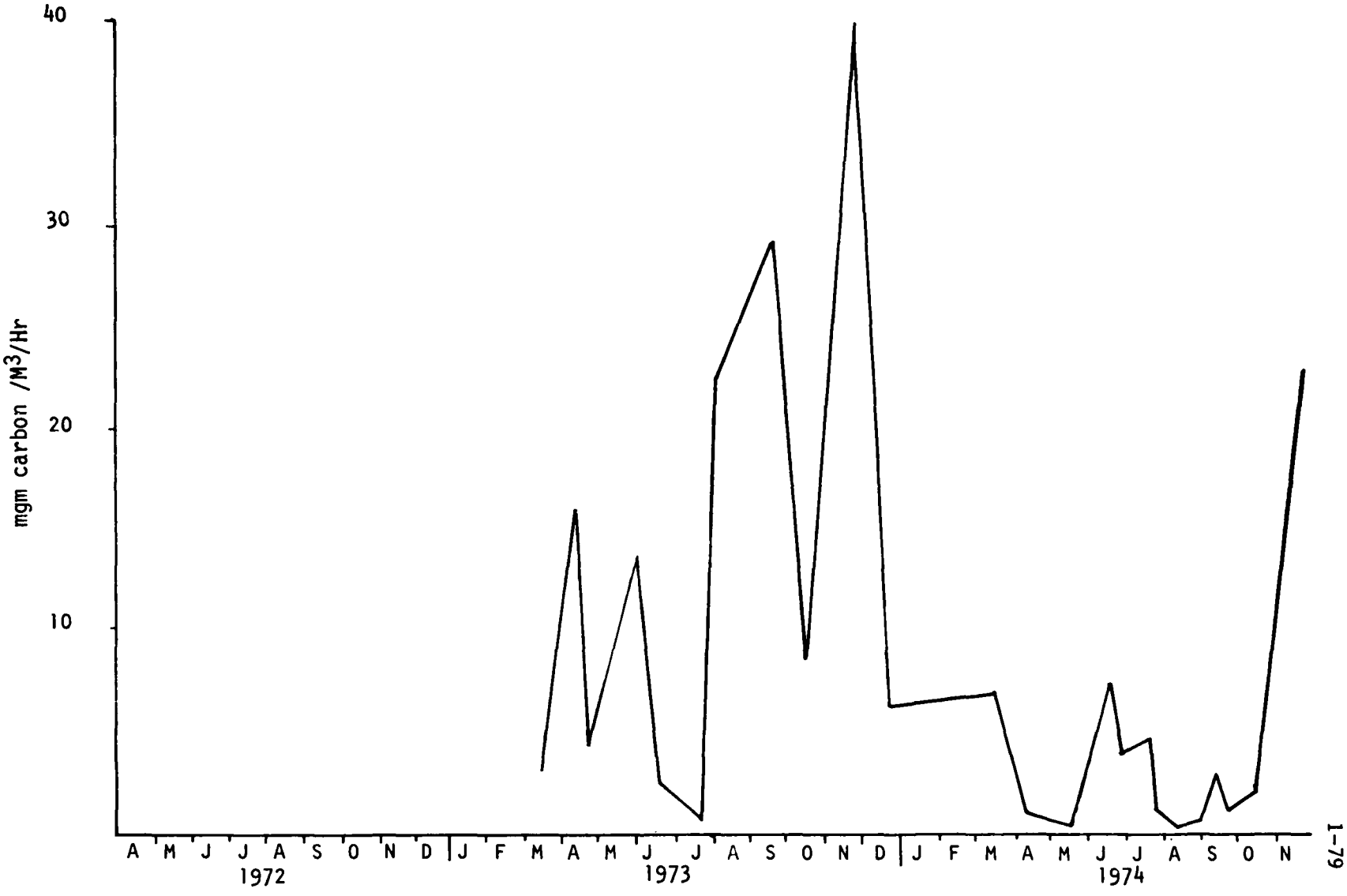


Figure 40. Mean carbon uptake in the 0-40 foot layer at EC-4 in Dworshak Reservoir, 1973-1974, as measured by the carbon-14 method.

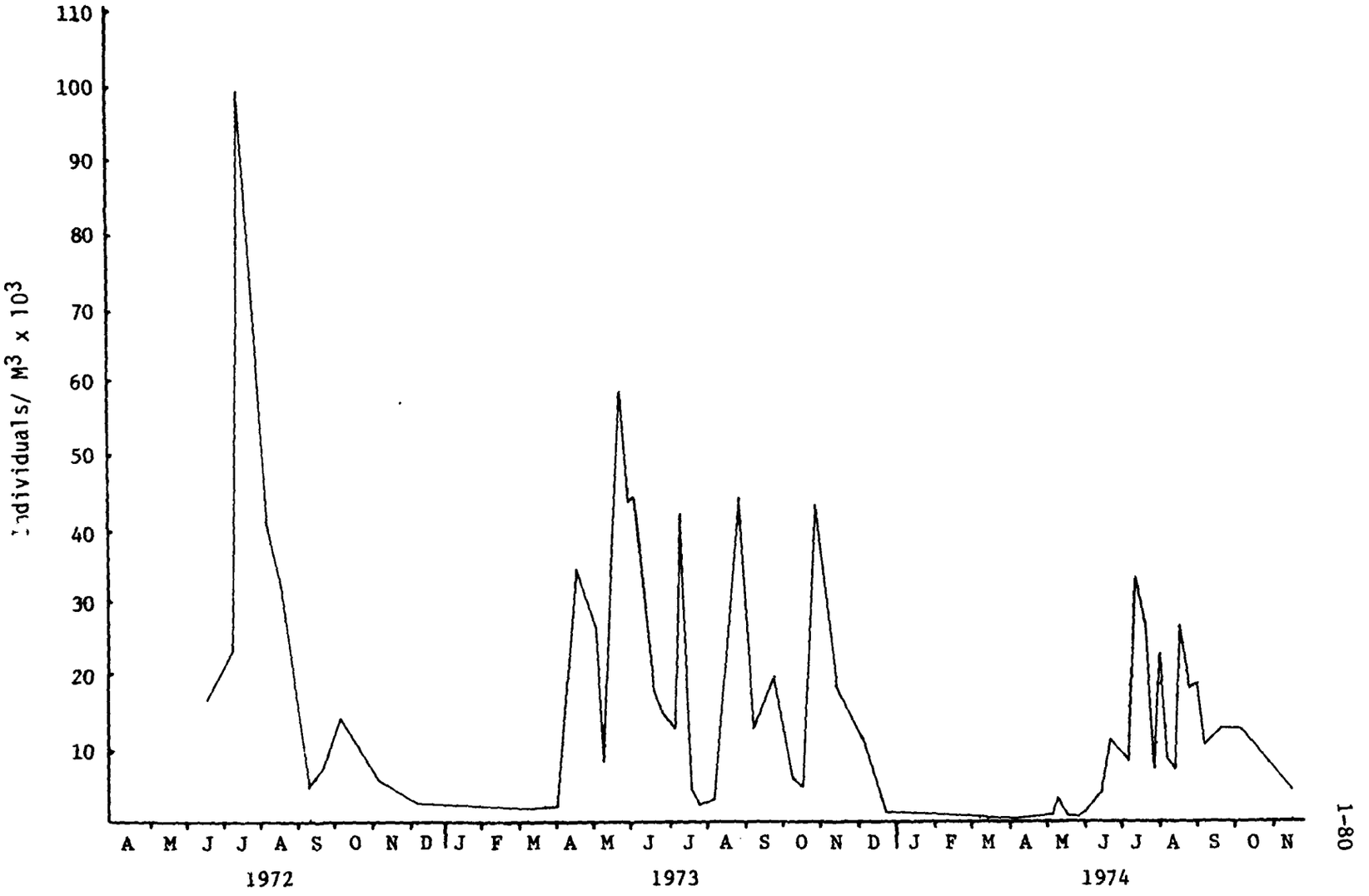


Figure 41. Mean total zooplankton in the 0-40 foot layer at RM 3 in Dworshak Reservoir, 1972-74.

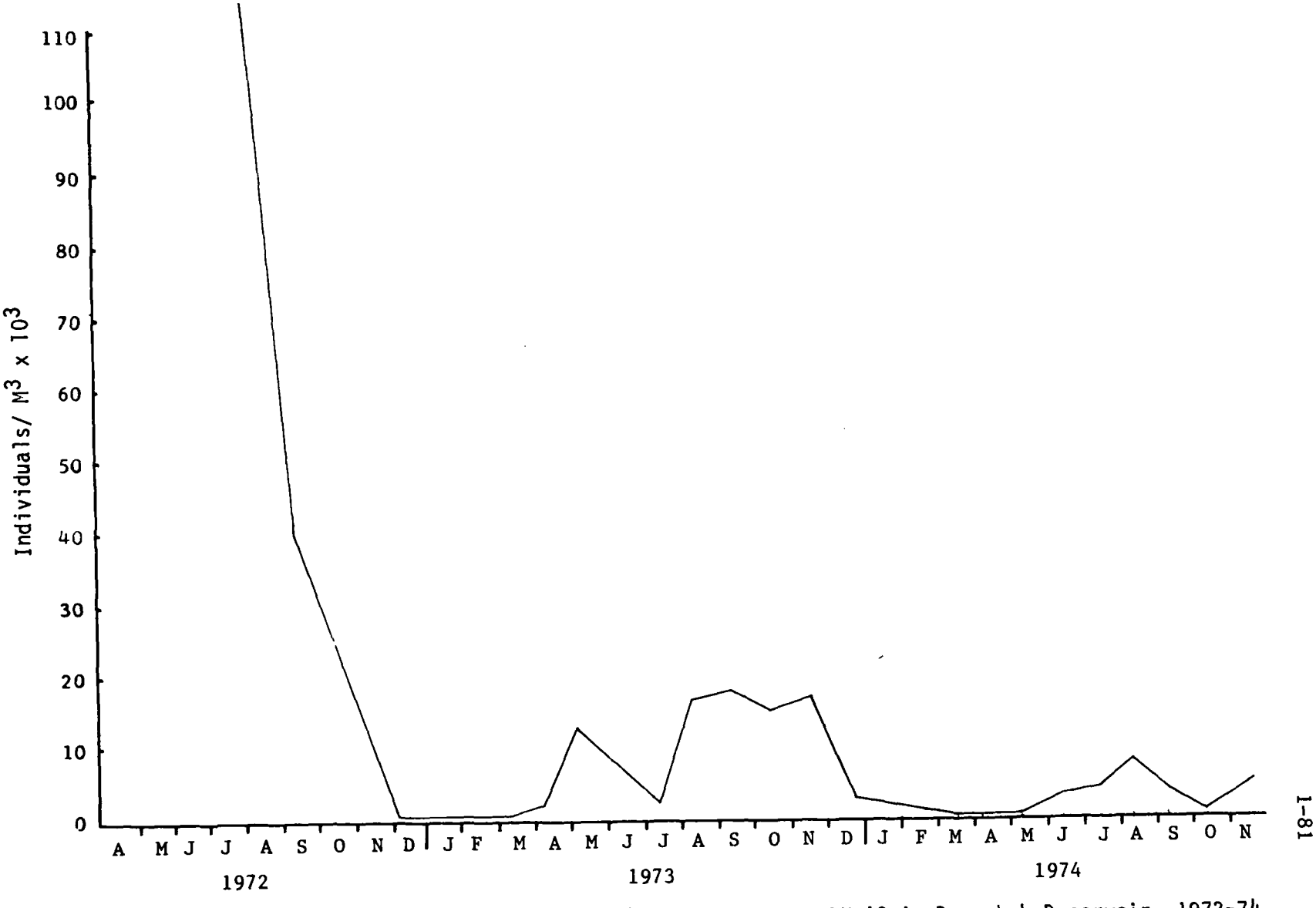


Figure 42. Mean total zooplankton in the 0-40 foot layer at RM 19 in Dworshak Reservoir, 1972-74.

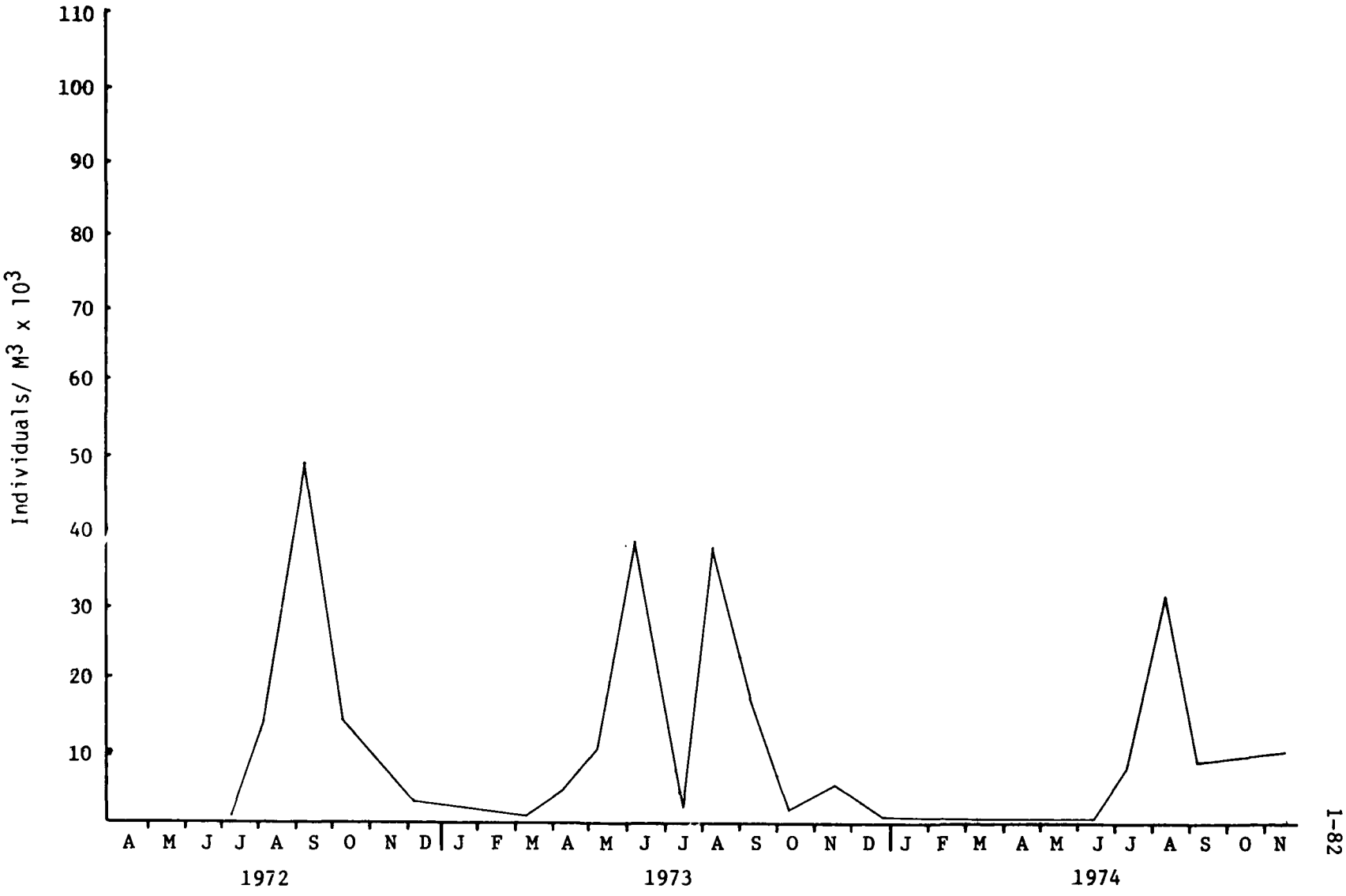


Figure 43. Mean total zooplankton in the 0-40 foot layer at RM 35 in Dworshak Reservoir, 1972-74.

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PART 2 IMPACT OF L (U) IDAHO UNIV MOSCOW
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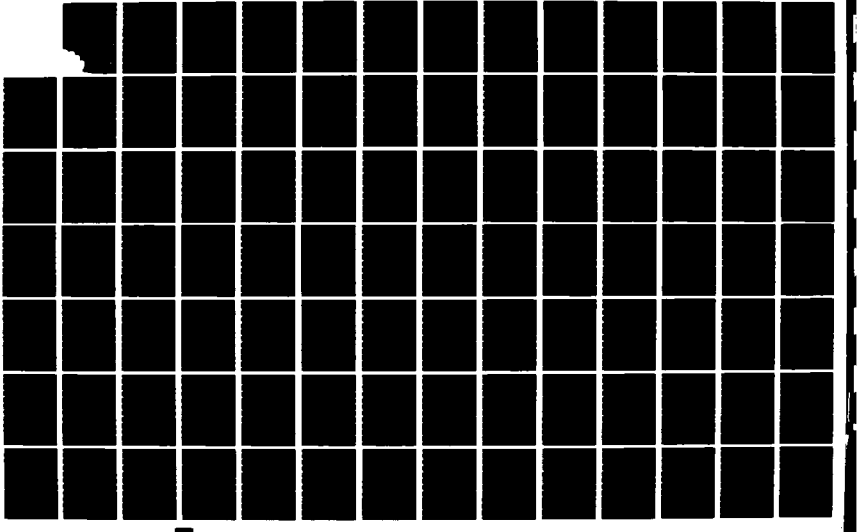

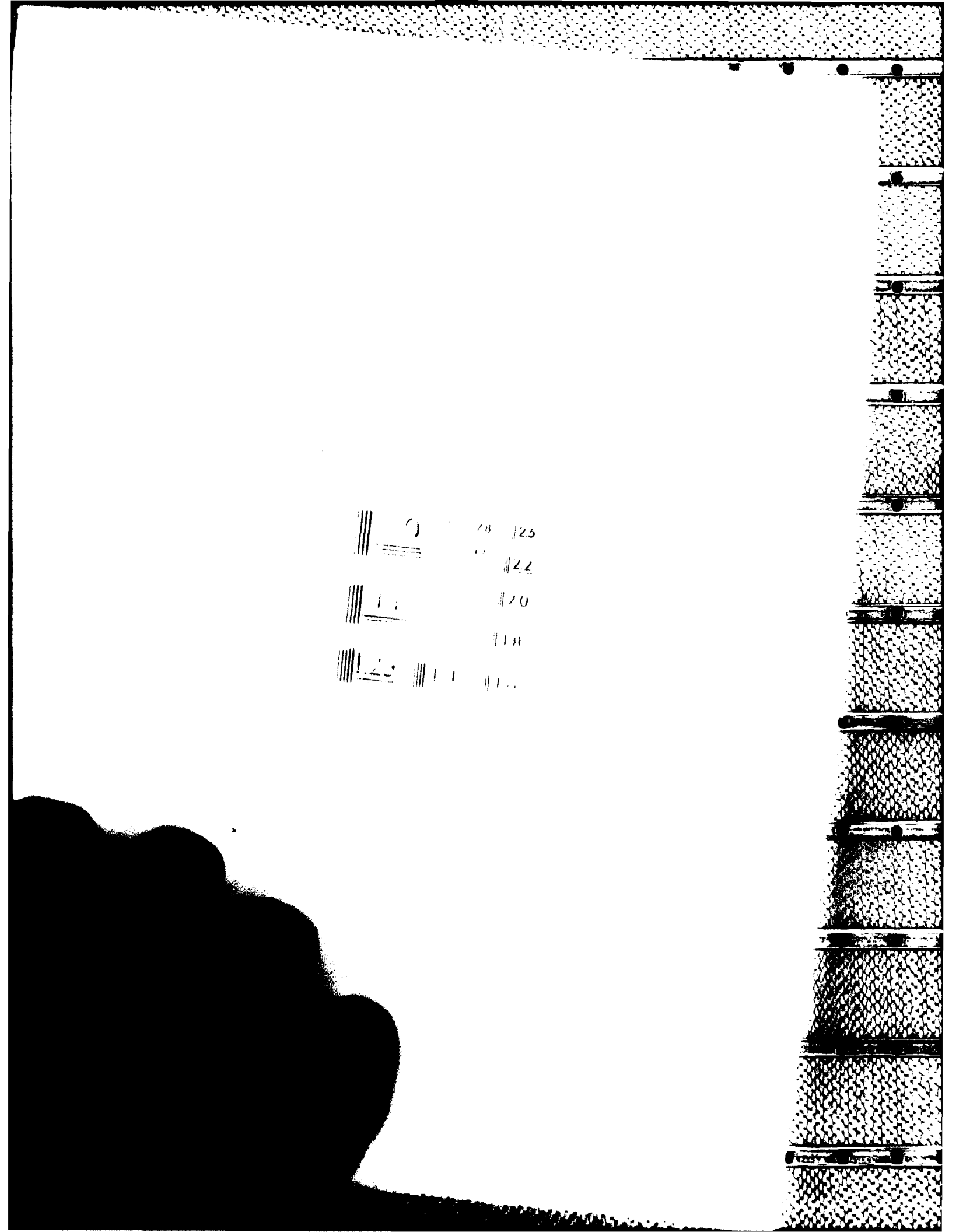

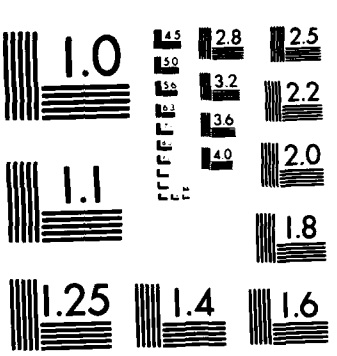

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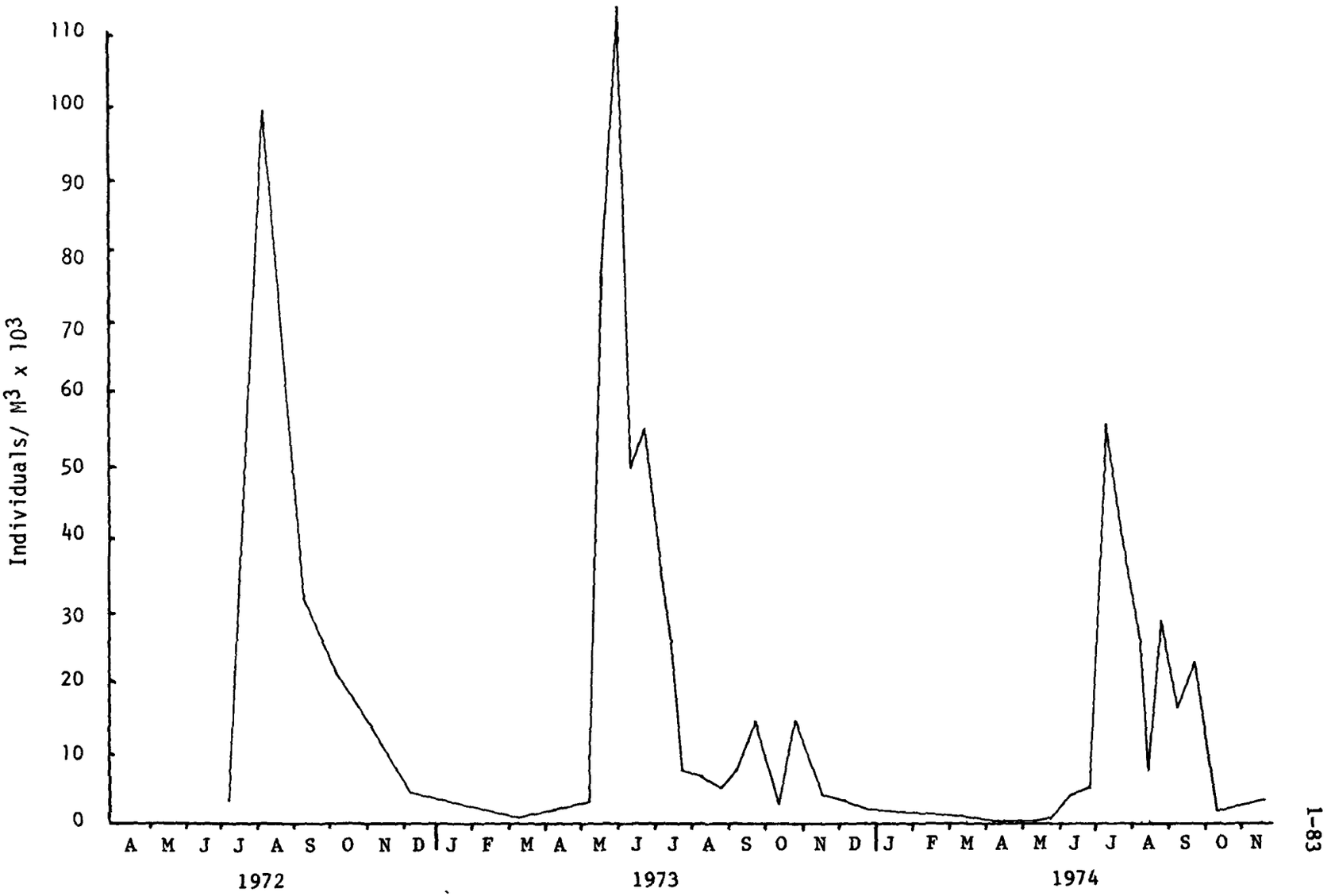

Figure 44. Mean total zooplankton in the 0-40 foot layer at EC-4 in Dworshak Reservoir, 1972-74.

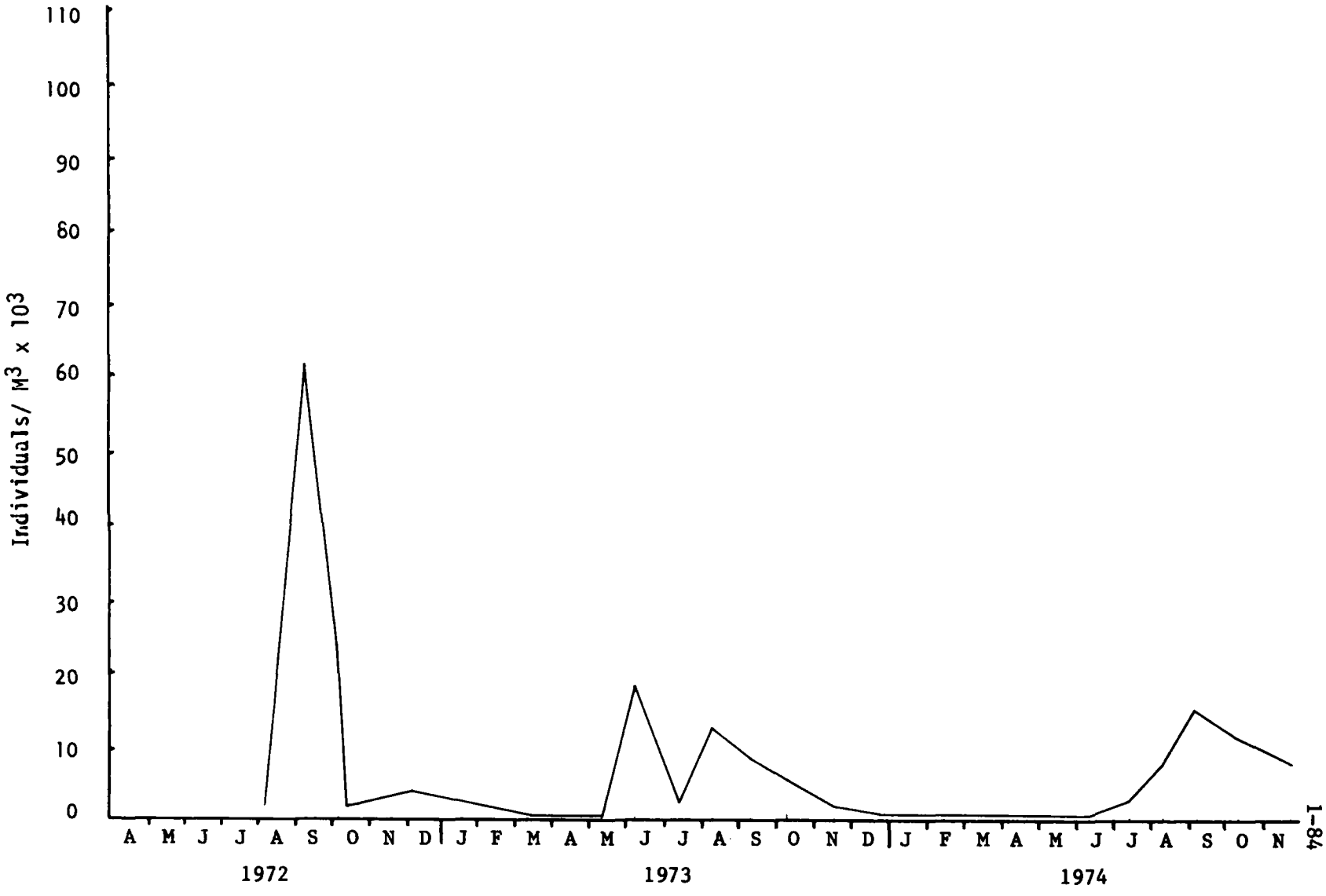

Figure 45. Mean total zooplankton in the 0-40 foot layer at LNF-1 in Dworshak Reservoir, 1972-74.

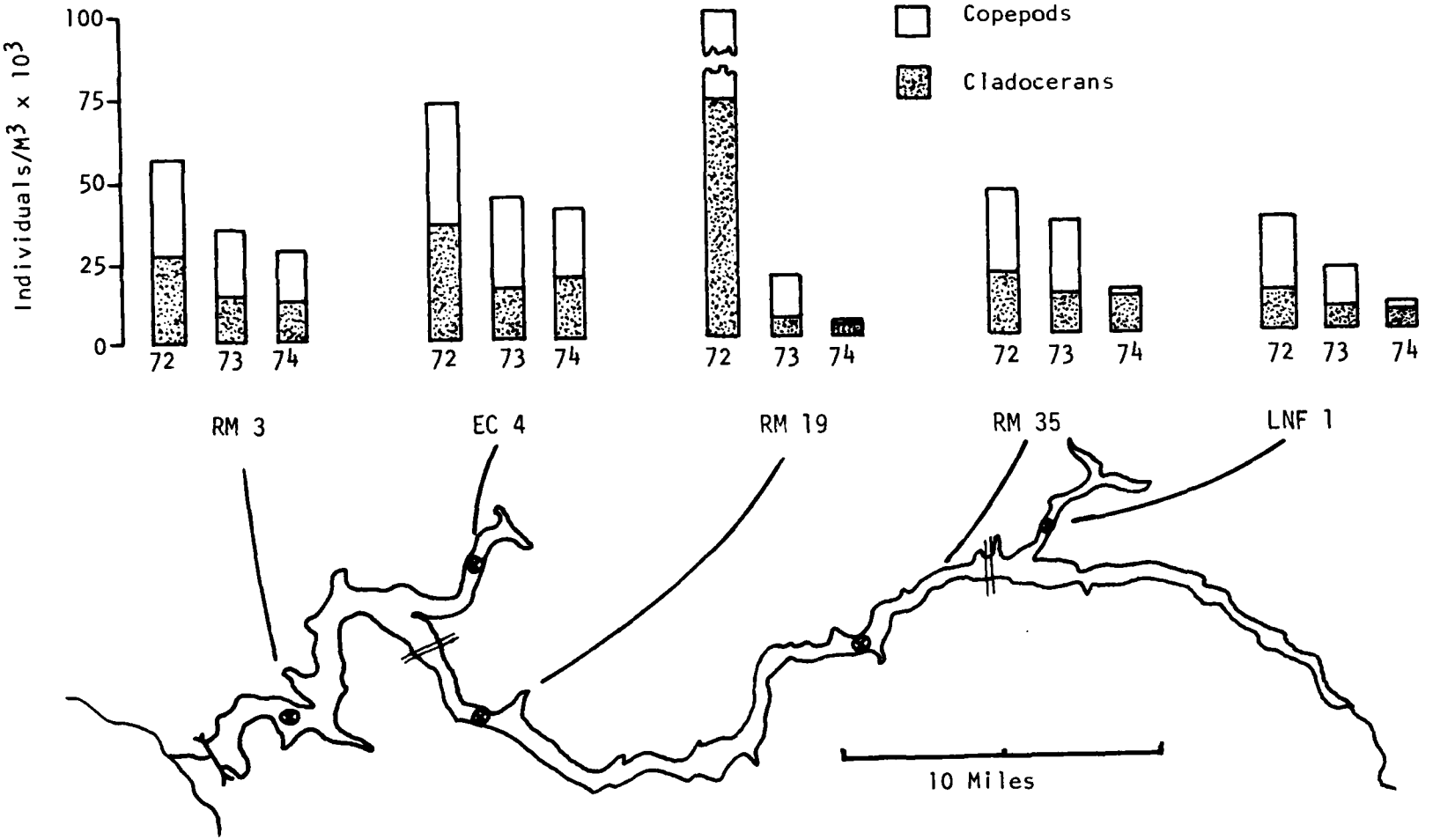

Figure 46. Mean Summer-Fall (June-October) zooplankton composition in the 0-40 foot layer of Dworshak Reservoir, 1972-74.

were fewer measurable fast rises in numbers followed by abrupt die-offs in 1974. This indicates an increase in population stability.

Chydorus sphaericus, Bosmina longirostris, and Ceriodaphnia sp. were the first species to occur in the reservoir in the summer of 1972. By the end of that first year, Cyclops bicuspidatus, Diaphanosoma, Daphnia schodleri, D. rosea, D. galeata-mendotae, and D. pulex were established components of the community. No new species were added until July, 1974 when Polyphemus appeared, followed by Holopedium in August. We found no Calanoid copepods in Dworshak Reservoir. The mean number of zooplantkon species per sample decreased from 4.79 in 1972 to 3.65 and 3.67 in 1973 and 1974. This decline is difficult to explain since greater variability in the phytoplankton community should result in great zooplankton species diversity. However, the shift in 1974 to a mid-summer pre-dominance of dinoflagellates and the occurrence of an additional bluegreen algae (Aphanizomenon) may have forced declines of some zooplankton forms. Also, little is known about the effect of fish predation in Dworshak and possible selection for certain species of zooplankton on population structure.

As with phytoplankton, zooplankton also seemed to be depressed at least indirectly, by high turbidities in the spring of 1974. In 1973, RM 19 had an early May pulse of 12×10^3 individuals/m^3; this pulse was totally absent in 1974. Similarly, we observed a late May, 1973 pulse of 37×10^3 individuals/m^3 at RM 35. This pulse was also totally absent in 1974. Egg production at each site began to increase with the initiation of a pulse, but fell back to winter levels, apparently as lack of food supply limited further population development (Figure 47).

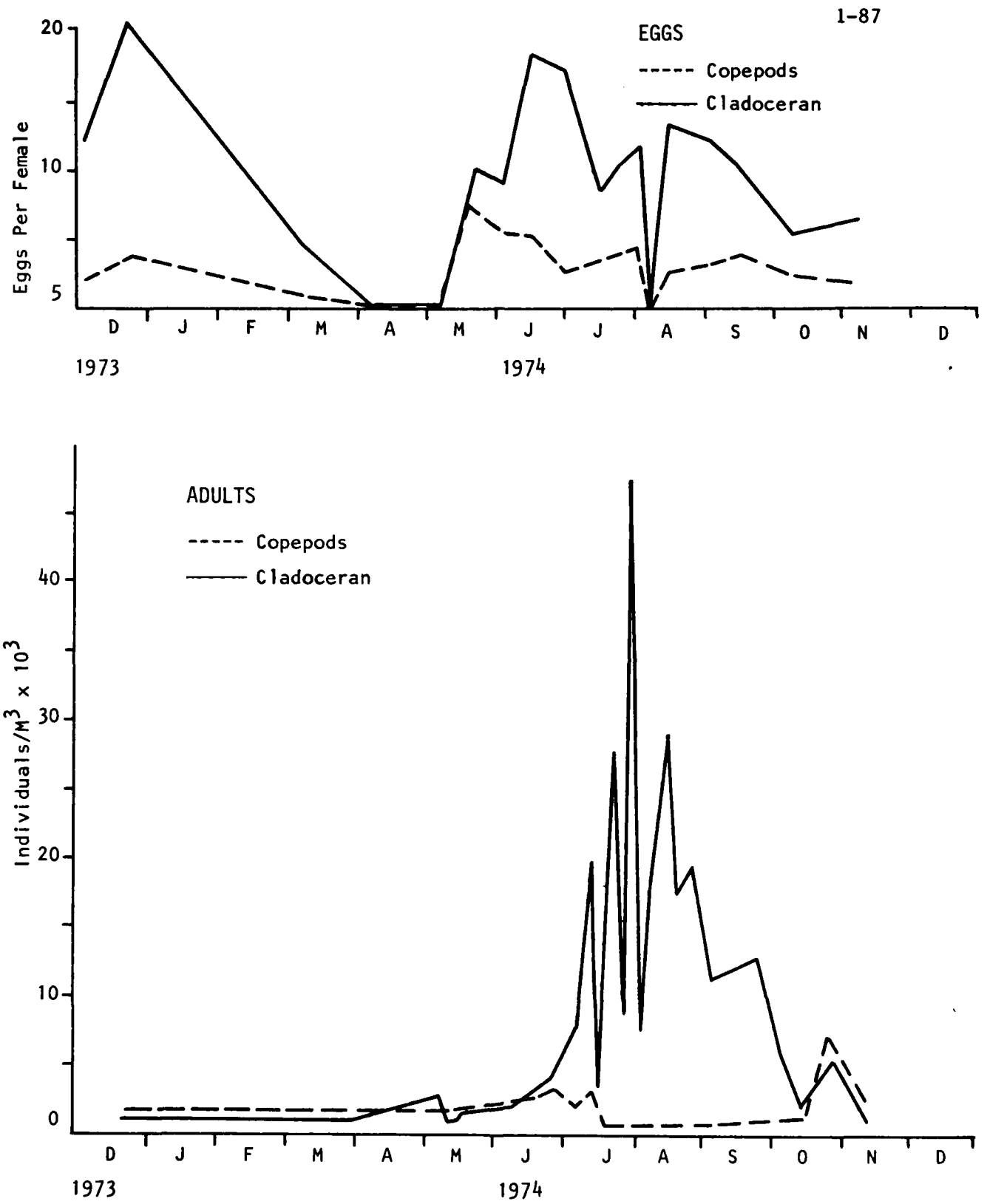

Figure 47. Zooplankton egg and adult counts in the 0-40 foot stratum of Dworshak Reservoir at Rm 3, 1974.

Regression Analyses

Relationships between limnological variables in Dworshak Reservoir were delineated with the SAS package computerized multiple correlation technique. Simple correlation coefficients between selected limnological variables for each site were presented in Tables 19-23. There were insufficient samples to partition analyses into spring, summer, and fall seasons so each year was analysed as a unit. These simple correlation coefficients simply express the average relationship between any two variables when separated from all other factors.

Multiple correlation coefficients for the relationships between a certain variable and a selected array of independent variables selected by the Stepwise Regression Analysis are presented in Tables 24-34. In 1974, the RM 3 spring diatom pulse was in May, five weeks later than in 1973 and nine weeks later than in 1973 at RM 19 and RM 35. It appears that when 1974 phytoplankton development did begin, population development was suppressed by the relatively cool surface water in the epilimnion that year.

We believe that nutrient limitation was the major factor in the 1973 decline in algal production since nitrate and phosphate levels dropped to detection limits intermittently through the summer-fall periods. Low levels of production in 1974, however, probably did not result from low nutrients since concentrations of all dissolved nutrients measured increased and because of the strong relationships of total algae and diatoms to temperature and turbidity. Turbidity is suggested as the major cause of low algal production in 1974, followed by low temperature suppression of production.

Our posed, but untested hypothesis is that 1974 algal production in Dworshak Reservoir was at first suppressed by high turbidity, then limited through the summer by low surface temperatures.

Table 19. Simple correlation coefficients between selected limnological variables at RM 3 in Dworshak Reservoir, 1972-74.

	Tot Algae	Green	Bluegreen	Diatoms	Zooplank	POC	Bact	O-PO_4	NO_3	SO_4	HCO_3	Light	Productivity	Temp
Tot Algae	*1.0*	*.08*	*.98***	*-.002*	*.87***	*.55s*	*.90***	*-.11*	*.04*	*.90**	*-.43**	*-.74ss*		*.27s*
	1.0	.09	-.07	.96**	-.07	-.03	-.02	-.07	-.17	.13	-.24	-.03	-.25ss	-.27*
	1.0	-.02	.86**	.30**	-.07	.03	-.24s	-.11	-.16	.55ss	.23*	.08	.26	.06
Green		*1.0*	*-.07*	*.61***	*-.17*	*-.25*	*-.08*	*-.58*	*.23*	*.96***	*.13*	*-.40*		*.07*
		1.0	-.08	-.16s	-.13	-.07	.14	-.20	-.16	.29	-.04	-.11	-.01	.31*
		1.0	-.19ss	.11	-.003	-.16	.15	.34	.42**	-.20	-.30**	-.07	-.10	.03
Bluegreen			*1.0*	*-.10*	*.89***	*.58s*	*.90***	*.88**	*.0003*	*-.25*	*.45**	*-.51*		*.23s*
			1.0	-.19ss	-.15	-.07	.04	-.19	-.18	-.23	.21ss	.24ss	.08	.46**
			1.0	-.14s	-.02	-.06	-.21s	-.05	-.12	.91**	.20ss	.03	.14s	.07
Diatoms				*1.0*	*-.24*	*-.26*	*-.001*	*-.41*	*.24*	*.99***	*-.28s*	*-.20*		*.25s*
				1.00	-.02	.002	-.06	.006	-.10	.14	-.25	-.03	-.25ss	-.41**
				1.00	-.23s	-.01	-.16	-.21	-.12	-.20	.19ss	.02	.29**	-.15s
Zooplank					*1.00*	*.87**	*.80***	*-.64s*	*-.27*	*.28*	*-.53**	*.83**		*.47ss*
					1.00	.06	-.22	.37*	-.10	-.43s	.20s	.18	.37*	.26ss
					1.00	-.31s	.05	-.003	-.25s	-.21	-1.8	.27	-.07	.59**
POC						*1.00*	*.74**	*-.61*	*-.50*	*.99ss*	*-.30*	*.95**		*.61s*
						1.00	-.37*	.02	.58**	-.06	-.09	.14	.38ss	-.23s
						1.00	-.01	-.13	-.09	-.30	.13	-.15	-.03	-.23s
Bact							*1.00*	*-.08*	*-.40*	*-.06*	*-.64**	*.35*		*.28*
							1.00	-.13	-.14	-.14	.52**	.02	-.22	.22
							1.00	-.004	.14	-.31	-.09	-.20	-.20	.006
O-PO_4								*1.00*	*.72s*	*-.38*	*.04*	*-.01*		*-.52*
								1.00	.50	.19	-.19	.13	-.01	-.27
								1.00	.10	-.02	-.17	-.03	-.26	.20
NO_3									*1.0*	*.27*	*.17*	*-.64s*		*-.40s*
									1.0	-.01	-.50**	.25s	-.16	-.55**
									1.0	.15	-.42**	-.31s	-.19	-.34*
SO_4										*1.00*		*-.26*		*.27*
										1.00	-.26	-.06	-.42s	-.08
										1.00	-.02	-.15	.58*	-.15
HCO_3											*1.00*	*.30*	*.78*	*-.21*
											1.00	.02	.20s	.48**
											1.00	.36		-.13
Light												*1.00*		*.87**
												1.00	-.08	.24ss
												1.00	.23ss	.51**
Productivity													*1.00*	*-.12*
													1.00	.18s
													1.00	.02
Temp														*1.00*
														1.00
														1.00

Levels of Significance:

s . . . . . P ≤ 0.20
ss . . . . . P ≤ 0.10
* . . . . . P ≤ 0.05
** . . . . . P ≤ 0.01

Legend of Types:

1972
1973
1974

Table 20. Simple correlation coefficients between selected limnological variables at RM 19 in Dworshak Reservoir, 1972-74.

	Tot Algae	Green	Bluegreen	Diatoms	Zooplank	POC	Bact	O-PO_4	NO_3	SO_4	HCO_3	Light	Temp
Tot Algae	*1.00*	*.99***	*-.17*	*-.07*	*-.24*	*-.06*	*-.18*	*-.94*	*-.62ss*	*-.57*	*-.26*	*-.29*	*.23*
	1.00	.14	.33*	.62**	-.09	.70*	-.31	-.11	-.31	-.25	.14	.04	.12
	1.00	.43*	.94**	.72**	.99**	-.09	-.11	-.24	-.23	.14	-.11	.58	.40*
Green		*1.00*	*-.15*	*-.24*	*-.35*	*-.15*	*-.14*	*-.94*	*-.58ss*	*-.64*	*-.27*	*-.41*	*.10*
		1.00	-.08	-.16	-.16	-.47	-.20	-.31	-.37	-.27	-.36*	.28	.39*
		1.00	-.06	-.06	-.06	-.11	-.12	.23	.59*	.23	-.55*	-.10	.02
Bluegreen			*1.00*	*-.16*		*-.60s*	*-.13*		*.27*		*-.11*	*-.30*	*-.19*
			1.00	-.16	.43ss	.37	-.12	-.22	-.26	-.24	.03	.27	.56**
			1.00	.12	.99**	-.09	-.10	-.23	-.21	.12	-.07	.60	.39ss
Diatoms				*1.00*	*.77ss*	*.57s*	*-.19*		*-.10*	*.99***	*.08*	*.83**	*.68***
				1.00	-.21	.54s	-.23	.09	-.05	-.08	.22s	-.19	-.37*
				1.00	.06	.75**	-.13	-.28	-.21	-.21	-.03	.58	-.20
Zooplank					*1.00*	*.37*	*-.40*	*-.95*	*.39*	*.49*	*.65*	*.97***	*.98***
					1.00	-.45	-.21	-.52s	-.59*	-.46	-.26	.10	.50*
					1.00	-.09	-.1:	-.24	-.22	.13	.08	.58	.36
POC						*1.00*	*-.31*	*-.67*	*.33*	*.94**	*.77ss*	*.26*	*.60*
						1.00	-.55s	.11	.02	.62s	.42	.53	-.06
						1.00	-.09	-.41s	-.31	-.26	.61		-.31
Bact							*1.00*		*.06*	*-.41*	*-.34*	*.44*	*.31*
							1.00	.36	.59ss	.61ss	-.25	-.29	-.20
							1.00	-.19	-.36	-.40	-.55	.62	-.05
O-PO_4								*1.00*	*.99ss*				
								1.00	.91**	.56ss	.07	-.17	-.51s
								1.00	.63**	.48*	-.84*	.59	-.53*
NO_3									*1.00*	*.56*	*.21*	*.66s*	*.02*
									1.00	.33	.18	-.21	-.68*
									1.00	.24	-.91*	-.83	-.42s
SO_4										*1.00*	*.95**	*.48*	*.58*
										1.00	-.41s	-.24	-.23
										1.00	.96**	-.78	-.02
HCO_3											*1.00*	*.66s*	*.05*
											1.00	-.17	-.26s
											1.00	-.91	.50*
Light												*1.00*	*.91**
												1.00	.59*
												1.00	.83
Temp													*1.00*
													1.00
													1.00

Levels of significance:

s . . . . . P ≤ 0.20
ss . . . . . P ≤ 0.10
* . . . . . P ≤ 0.05
** . . . . . P ≤ 0.01

Legend of Types:

1972
1973
1974

Table 21. Simple correlation coefficients between selected limnological variables at RM 35 in Dworshak Reservoir, 1972-74.

	Tot Algae	Green	Bluegreen	Diatoms	Zooplank	POC	Bact	O-PO_4	NO_3	SO_4	HCO_3	Light	Temp
Tot Algae	*1.000*	*.14*	*.37s*	*.74***	*.76**	*.01*	*-.25*	*.52*	*-.56s*		*.06*	*.16*	*.42s*
	1.00	-.01	.96**	.80**	.76**	.22	-.03		-.45s	-.31	-.04	.61*	.63**
	1.00	-.11	-.01		.91**	.03	.10	-.21	-.16	-.20	-.07	.14	.58**
Green		*1.00*	*-.18*	*-.25*	*-.23*	*.02*	*.37*	*-.90ss*	*-.24*		*-.47ss*	*.23*	*-.66***
		1.00	-.03	.004	.03	-.36	-.01		-.22	-.01	.08	.73**	.35s
		1.00	.08	-.13	-.45	.50s	-.10	-.27	-.28	.19	.12	-.24	-.66**
Bluegreen			*1.00*	*-.16*	*.04*	*.80ss*	*-.10*	*.05*	*-.13*		*.07*	*.83s*	*.54**
			1.00	.67**	.65*	.27	.04		-.34	-.24	.06	.66*	.61**
			1.00	-.08	.99**	-.27	-.17	-.15	-.17	-.10	-.21	.87**	.28s
Diatoms				*1.00*	*.94***	*-.72s*	*-.39*	*.81s*	*-.33*		*.27*	*-.53*	*.43s*
				1.00	.18	-.29	-.29		-.45s	-.30	-.10	-.10	.46*
				1.00	.63	.28	.28	-.19	-.14	-.19	-.06	-.16	.51**
Zooplank					*1.00*	*.54*	*-.46*	*1.00*	*-.38*		*.10*	*.88*	*.44*
					1.00	-.12	-.11		-.19	-.08	-.18	.48	.60*
					1.00	.61	.06		-.33	-.24	.27	.97**	.91*
POC						*1.00*	*.17*	*-.43*	*.11*		*.21*	*.98s*	*.22*
						1.00	.50s		-.61*	-.63*	-.06	-.06	.22
						1.00	.22	-.35	-.09	.39	.79**	.33	-.06
Bact							*1.00*		*.55*		*-.62s*	*.88*	*-.04*
							1.00		-.38	-.31	.32	-.27	.16
							1.00	.13	.22	-.21	.07	-.07	.50ss
O-PO_4								*1.00*	*.04*		*.77*		*.91ss*
								1.00					
								1.00	.19	-.31	-.13	-.12	.19
NO_3									*1.00*		*.14*	*.27*	*.24*
									1.00	.64*	.12	-.36	-.77**
									1.00	-.33	-.30	.13	.10
SO_4										*1.00*			
										1.00	.28	-.22	-.43s
										1.00	.40s	-.06	-.13
HCO_3											*1.00*	*.16*	*.40s*
											1.00	-.34	.01
											1.00	.24	.10
Light												*1.00*	*.58*
												1.00	.76**
												1.00	.43s
Temp													*1.00*
													1.00
													1.00

Levels of significance:

s . . . . . P ≤ 0.20
ss . . . . . P ≤ 0.10
* . . . . . P ≤ 0.05
** . . . . . P ≤ 0.01

Legend of Types:

1972
1973
1974

Table 22. Simple correlation coefficients between selected limnological variables at EC 4 in Dworshak Reservoir, 1972-74.

	Tot Algae	Green	Bluegreen	Diatoms	Zooplank	POC	Bact	$O\text{-}PO_4$	NO_3	SO_4	HCO_3	Light	Temp
Tot Algae	*1.000*	*.72**	*-.24*	*.54s*	*.56s*	*.80**	*-.36*	*-.31*	*.10*		*.36*	*-.33*	*.33*
	1.000	.72**	.20s	.70**	.23	.05	.004	-.17	-.32	-.18	-.15	.33*	.03
	1.000	.94**	.26s	.01	.36s	.04	.14	-.03	-.03	.32	.03	.25s	.35*
Green		*1.000*	*-.19*	*-.20*	*-.14*	*.70s*	*-.29*	*-.32*	*.06*		*-.10*	*-.30*	*-.19*
		1.000	.14	.03	.21	.05	-.001	-.14	-.19	-.19	-.26s	.30ss	.38**
		1.000	-.07	-.05	.44*	-.02	.22	-.20	-.14	-.31	-.06	.16	.30*
Bluegreen			*1.000*	*-.11*	*-.20*		*.17*		*.18*		*.24*		*.35*
			1.000	-.06	-.08	-.10	-.15	-.14	-.24	-.20	.10	.17	.33*
			1.000	.09	-.12	.15	-.21	.41ss	-.21	.35	.29ss	.38*	.19s
Diatoms				*1.000*	*.96***	*.24*	*-.17*	*.24*	*.07*		*.61s*	*-.12*	*.68ss*
				1.000	.13	.09	.11	-.10	-.28	-.03	-.14	.21	-.17
				1.000	-.37s	.19	.22	-.31s	-.31s	.23	-.17	.20	-.32*
Zooplank					*1.000*	*.20*	*-.26*	*-.10*	*-.006*		*.70**	*-.03*	*.68ss*
					1.000	-.22	.07	.35s	-.16	-.13	.06	.61**	.37*
					1.000	-.38s	-.09	.13	-.23	-.09	.27s	.28	.54**
POC						*1.000*	*-.25*	*-.48*	*-.37*		*.24*	*-.28*	*.18*
						1.000	-.33s	.43ss	.33s	.17	.35s	.24	-.29
						1.000	-.48ss	.38	.05	.85**	-.14	.20	-.19
Bact							*1.000*	*-.51*	*-.31*		*-.47*	*.99***	*-.27*
							1.000	-.20	-.30s	-.13	-.24	.48ss	.29
							1.000	-.50*	.30	-.33	.30s	-.15	-.04
$O\text{-}PO_4$								*1.000*	*.55*		*-.82s*	*-.79*	*-.61*
								1.000	.57**	-.01	-.38s	.05	-.40*
								1.000	.28s	.29	.03	.03	.31s
NO_3									*1.000*		*-.08*	*-.43*	*.09*
									1.000	.03	-.37ss	-.38s	-.68**
									1.000	-.27	.15	-.45ss	.11
SO_4										*1.000*			
										1.000	-.34	-.10	-.19
										1.000	.23	.08	-.15
HCO_3											*1.000*	*.47*	*.91***
											1.000	.17	.44**
											1.000	.08	.33*
Light												*1.000*	*.45*
												1.000	.44**
												1.000	.61**
Temp													*1.000*
													1.000
													1.000

Levels of significance:

s . . . . . $P \leq 0.20$
ss . . . . . $P \leq 0.10$
* . . . . . $P \leq 0.05$
** . . . . . $P \leq 0.01$

Legend of Types:

1972
1973
1974

Table 23. Simple correlation coefficients between selected limnological variables at LNFK 1 in Dworshak Reservoir, 1972-74.

	Tot Algae	Green	Bluegreen	Diatoms	Zooplank	POC	Bact	O-PO4	NO3	SO4	HCO3	Light	Temp
Tot Algae	*1.00*	*-.45*	*.56s*	*.61ss*	*-.15*	*.33*	*.10*	*.62*	*-.80*		*.32*	*.07*	*.93***
	1.00	-.05	-.05	.99**	.16		-.26		-.48	-.37	.08	.97*	.49s
	1.00	-.15	.004	.73**	.99*	-.17	.03	-.10	-.34s	.12	.28	.14	.39s
Green		*1.00*	*-.29*	*-.25*	*.93***	*.65s*	*.24*	*.38*	*.18*		*.73*	*.71*	*.11*
		1.00	-.13	-.20	.33		.75s		-.07	-.40	-.0001		.39
		1.00	-.09	-.16	-.48	-.36	-.04	-.18	.17	.20	-.07	-.23	-.49*
Bluegreen			*1.00*	*-.32*	*-.31*	*-.11*	*-.22*		*-.41*		*-.15*	*.41*	*.89ss*
			1.00	-.04	-.23		.33		-.06	-.26	.48ss		.12
			1.00	-.04		.22	.93**	.09	-.12	-.25	-.17	-.12	.16
Diatoms				*1.00*	*.08*	*.44*	*.31*	*.60*	*-.52*		*.79*	*-.30*	*-.07*
				1.00	-.42		.32		-.46	-.33	.06	.95*	.40s
				1.00	.25	-.12	.29	-.06	-.33s	.18	.49*		.16
Zooplank					*1.00*	*.36*	*-.30*	*.66s*	*-.07*	*-.47*	*.32*	*.52*	*.26*
					1.00	.66	.09	.57ss	-.44s	-.09	.31	.88*	.63**
					1.00		-1.00		-.62	-.55	-.48	.93	.95s
POC						*1.00*	*.20*	*.44*	*.17*	*.40*	*.83**	*.63s*	*-.32*
						1.00	-.19	-.25	-.40	-.50	.03	-.38	.18
						1.00	.01	-.27	-.69ss	.66ss	.62*	-.19	-.25
Bact							*1.00*	*-.34*	*-.29*	*-.20*	*.46*	*.06*	*-.67*
							1.00	-.13	-.21	-.14	.07	-.38	.18
							1.00	.36s	-.27	-.36	-.15	-.29	.23
O-PO4								*1.00*	*-.32*	*-.32*	*.47*	*.12*	*.55*
								1.00	-.09	.14	-.21	.60	.24
								1.00	-.30	-.48*	-.23	.05	.34s
NO3									*1.00*	*.81ss*	*-.25*	*-.30*	*-.93**
									1.00	.41s	-.18	-.39	-.72**
									1.00	.36s	-.48*	.20	-.38s
SO4										*1.00*	*.62*		*-.97**
										1.00	.41s	-.18	-.46ss
										1.00	*.63***	*-.18*	*-.22*
HCO3											*1.00*	*.97s*	*-.29*
											1.00	-.09	.38s
											1.00	-.20	-.11
Light												*1.000*	*.68*
												1.00	.64*
												1.00	.69**
Temp													*1.000*
													1.00
													1.00

Levels of significance:

s . . . . . P ≤ 0.20
ss . . . . . P ≤ 0.10
* . . . . . P ≤ 0.05
** . . . . . P ≤ 0.01

Legend of Types:

1972
1973
1974

Table 24. The relationship of percent oxygen saturation to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
RM 3	1973	Bacteria, Zooplankton, POC[1], Ortho PO_4, NO_3, Conductivity and Turbidity.	.550	Conductivity	.009	10
			.676	Conductivity, Bacteria	.011	10
			.817	Bacteria, Zooplankton, Conductivity	.006	10
			.874*	Bacteria, Zooplankton, Conductivity, POC	.008	10
RM 3	1973	Bacteria, Zooplankton, Total Algae, NO_3, Conductivity and Turbidity	.640*	Conductivity	.056	5
RM 3	1974	Bacteria, Zooplankton, Total Algae, Ortho-PO_4, NO_3, Conductivity and Turbidity.	.184	NO_3	.030	24
			.361	NO_3, Turbidity	.0030	24
			.479*	NO_3, Turbidity, Conductivity	.0032	24
RM 19	1972	Bacteria, Total Algae, Conductivity, and Turbidity.	.556	Turbidity	.0534	6
			.714	Bacteria, Turbidity	.0826	6
			.851*	Bacteria, Total Algae, Turbidity	.0933	6
RM 19	1973	Total Algae, Conductivity and Turbidity.	.329	Total Algae	.0007	32
RM 35	1972	Total Algae and Conductivity.	.422*	Conductivity	.0012	13
RM 35	1973	Total Algae and Turbidity.	.296	Turbidity	.0127	19
RM 35	1974	Total Algae, Bacteria, Ortho PO_4, NO_3 POC, Conductivity and Turbidity.	.530	Bacteria	.0398	7
EC 4	1973	Bacteria, Zooplankton, Total Algae, Ortho PO_4, NO_3, Conductivity and Turbidity.	.420	Bacteria	.081	7
			.683	Bacteria, Total Algae	.057	7
			.872	Bacteria, Total Algae, Zooplankton	.032	7
			.946	Bacteria, Zooplankton, Ortho PO_4, NO_3	.030	7
			.980	Bacteria, Zooplankton, Total Algae, Ortho PO_4, NO_3	.049	7
EC 4	1974	Bacteria, Zooplankton, Total Algae, Ortho-PO_4, NO_3, Conductivity and Turbidity.	.268	Total Algae	.067	12
			.452	Bacteria, Conductivity	.049	12
			.559*	Bacteria, Total Algae, Conductivity	.052	12
All stations	1973	Bacteria, Zooplankton, Total Algae, POC, NO_3, Conductivity, and Turbidity, Ortho PO_4	.264	NO_3	.008	24
			.528	NO_3, Conductivity	.001	24
			.595	Bacteria, NO_3, Conductivity	.001	24
			.661*	Bacterial, NO_3, Ortho PO_4, Conductivity	.001	24
All stations	1974	Zooplankton, Bacteria, Total Algae, POC, TOC[2] Ortho PO_4, NO_3, Conductivity and Turbidity	.477	Conductivity	.005	14
			.564	Conductivity, Total Algae	.007	14
			.632	Bacteria, POC, Conductivity	.010	14
			.751	Bacteria, POC, Conductivity, Turbidity	.005	14
			.843*	Bacteria, Zooplankton, POC, Conductivity, and Turbidity	.002	14

[1]POC = Persulfate oxidizable carbon

[2]POC = Total organic carbon

Table 25. The relationship of persulfate oxidizable carbon to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variables (s) Selected	Probability of Greater "F"	d.f.
RM 3	1973	Bacteria, NO_3, Ortho PO_4 and HCO_3.	.150	Bacteria	.022	33
			.303	Bacteria, Ortho PO_4	.004	33
			.350*		.005	33
EC 4	1973	Bacteria, NO_3, and Ortho PO_4,	.188	Ortho PO_4	.069	17
EC 4	1973	Bacteria, Total Algae, Zooplankton, NO_3, Ortho PO_4, Turbidity and HCO_3.	.425	HCO_3	.056	8
			.652*	Bacteria, HCO_3	.042	8
EC 4	1974	Bacteria, Zooplankton, NO_3, Ortho-PO_4, Turbidity and HCO_3.	.245	Bacteria	.069	13
All Stations	1972	Bacteria, Total Algae, Zooplankton and NO_3.	.253	Zooplankton	.005	29
			.314	Zooplankton, NO_3	.007	29
			.365*	Zooplankton, NO_3, Total Algae	.008	29
All Stations	1972	Bacteria, Total Algae, Zooplankton, NO_3, Ortho PO_4, Turbidity, HCO_3, and Conductivity.	.244	HCO_3	.144	9
			.726	HCO_3, Conductivity	.011	9
			.805	Ortho PO_4, HCO_3, Conductivity	.016	9
			.878*	Ortho PO_4, Turbidity, HCO_3, Conductivity	.018	9

Table 26. The relationship of ortho phosphate and bicarbonate to limnological varaibles selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
	$(O\text{-}PO_4)$					
EC 4	1974	Bacteria, Zooplankton and Total Algae.	.212	Bacteria	.081	14
	(HCO_3)					
RM 19	1972	Total Algae, Turbidity, and Conductivity.	.229	Turbidity	.095	12
			.408*	Turbidity, Total Algae	.072	12
RM 19	1973	Total Algae, Zooplankton, Turbidity and Conductivity.	.185	Turbidity	.093	15
			.301*	Zooplankton, Turbidity	.096	15
RM 19	1974	Bacteria, Total Algae, TOC[2], Ortho PO_4, NO_3, Turbidity and Conductivity.	.218	Bacteria	.175	9
			.496	Ortho PO_4, Conductivity	.041	9
			.741	Bacteria, Turbidity and Conductivity	.034	9
RM 3	1973	Total Algae, Turbidity and Conductivity.	.252*	Total Algae	.038	16
RM 3	1974	Bacteria, Total Algae, Zooplankton, POC[1], Ortho PO_4, NO_3, Turbidity and Conductivity.	.234	NO_3,	.022	21
			.415	NO_3, Conductivity	.004	21
			.560	NO_3, Total Algae, Conductivity	.002	21
			.610*	NO_3, Total Algae, Ortho PO_4, Conductivity	.002	21
RM 35	1972	Total Algae and Conductivity.	.319	Conductivity	.034	13
RM 35	1973	Total Algae, Turbidity and Conductivity.	.361*	Conductivity	.002	24
RM 35	1974	Bacteria, Total Algae, TOC, NO_3, Ortho-PO_4, Turbidity and Conductivity.	.603	TOC	.023	7
			.842*	TOC, Conductivity	.010	7
EC 4	1973	Total Algae, Zooplankton, Turbidity and Conductivity.	.290	Conductivity	.045	13
			.440*	Turbidity, Conductivity	.065	13
EC 4	1974	Total Algae, Zooplankton, Ortho PO_4, NO_3, Turbidity, Conductivity and Bacteria.	.353	Conductivity	.031	12
			.491	Turbidity, Conductivity	.034	12
All Stations	1972	Bacteria, Total Algae, Conductivity, Zooplankton and Turbidity	.230	Total Algae	.036	18
			.416*	Total Algae, Zooplankton	.013	18
All Stations	1972	Bacteria, Total Algae, Zooplankton, POC NO_3, Ortho PO_4, Turbidity and Conductivity.	.711	Zooplankton	.003	9
			.789	Zooplankton, Zooplankton	.005	9
			.874	Zooplankton, Zooplankton, POC	.005	9

[1]POC = Persulfate oxidizable carbon

[2]TOC = Total organic carbon

Table 27. The relationship of total algae to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Selected Variables (s)	Probability of Greater "F"	d.f.
RM 3	1972	Temperature, Turbidity, Conductivity and HCO_3.	.252	HCO_3	.038	16
RM 19	1974	Temperature, Turbidity, Conductivity, and HCO_3.	.166	Temperature	.019	31
			.213*	Conductivity, HCO_3	.030	31
RM 35	1972	Temperature, Conductivity and HCO_3.	.241	Conductivity	.072	13
RM 35	1973	Temperature, Turbidity, and HCO_3.	.605	Temperature	.001	15
			.787	Temperature, Turbidity	.001	15
			.874*	Temperature, Turbidity, HCO_3	.001	15
RM 35	1974	Temperature, Turbidity, Conductivity, and HCO_3.	.428	Temperature	.002	20
			.499*	Temperature, HCO_3	.002	20
LNFK I	1974	Temperature, TOC[1], Ortho PO_4, NO_3 Turbidity, SO_4, Fe, Si, and HCO_3.	.180	TOC	.128	13
			.406	Temperature, TOC	.056	13
			.595	Temperature, TOC, Si	.024	13
All Stations	1972	Temperature, Conductivity, HCO_3, Turbidity, Zooplankton, NO_3, Si and Total Algae.	.522	Zooplankton	.002	15
			.747*	HCO_3, Zooplankton	.001	15

[1]TOC = Total Organic Carbon

Table 28. The relationship of diatoms to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Selected Variables	Possibility of Greater "F"	d.f.
RM 3	1972	Temperature, Turbidity, Conductivity, and HCO_3.	.201	Temperature	.068	16
			.310*	Temperature, Turbidity	.073	16
RM 3	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, and Light (F.C.)	.091	Temperature	.237	16
			.286	Temperature, Conductivity	.093	16
			.471*	Temperature, Conductivity, Light (F.C.)	.035	16
RM 3	1974	Temperature, Ortho PO_4, NO_3, Turbidity, Conductivity, HCO_3 and Light (F.C.)	.166	HCO_3	.033	26
			.334	Turbidity, HCO_3	.008	26
			.429	Temperature, HCO_3, Light (F.C.)	.005	26
			.447*	Temperature, Turbidity, HCO_3, Light (F.C.)	.009	26
RM 19	1972	Temperature, Turbidity, Conductivity and HCO_3.	.481	Turbidity	.009	12
			.575	Turbidity, HCO_3	.014	12
RM 19	1973	Temperature, Turbidity, Conductivity, and HCO_3.	.237	Conductivity	.004	32
			.293*	Temperature, Conductivity	.006	32
RM 35	1972	Temperature, Conductivity and HCO_3.	.242*	Conductivity	.071	13
RM 35	1973	Temperature, Turbidity and HCO_3.	.360	Temperature	.014	15
			.529*	Temperature, Turbidity	.008	15
RM 35	1974	Temperature, Turbidity, Conductivity, and HCO_3.	.364	Temperature	.004	20
			.537	Temperature, HCO_3	.001	20
EC 4	1974	Temperature, Turbidity, Conductivity, and HCO_3.	.290	Turbidity	.001	40
			.435	Turbidity, Conductivity	.001	40
LNFK 1	1974	Temperature, TOC[1], Ortho PO_4, NO_3, Turbidity, SO_4, Fe, Si, and HCO_3.	.397	HCO_3	.015	13
			.591	TOC, HCO_3	.008	13
			.731*	TOC, Turbidity, HCO_3	.004	13
All Stations	1973	Temperature, Conductivity, HCO_3, Turbidity, Zooplankton, NO_3, and Si.	.208	Conductivity	.070	15
			.394*	Conductivity, NO_3	.040	15

[1]TOC = Total organic carbon

Table 29. The relationship of green algae to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
RM 3	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, and Light (F.C.).	.239	HCO_3	.044	16
			.535	HCO_3, Conductivity	.005	16
			.631	Temperature, HCO_3, Light (F.C.)	.004	16
			.752*	Temperature, Conductivity, HCO_3, Light (F.C.)	.002	16
RM 3	1974	Temperature, Ortho PO_4, NO_3, Turbidity, Conductivity, HCO_3, and Light (F.C.)	.223	Ortho PO_4	.012	26
			.346*	Ortho PO_4	.006	26
RM 19	1973	Temperature, Turbidity, Conductivity and HCO_3.	.805	Turbidity	.001	32
			.829*	Temperature, Turbidity	.001	32
RM 19	1974	Temperature, Turbidity, Conductivity and HCO_3.	.810	Temperature	.001	9
			.888*	Temperature, HCO_3	.001	9
RM 35	1972	Temperature, Conductivity and HCO_3.	.436*	Temperature	.010	13
RM 35	1973	Temperature, Turbidity, and HCO_3.	.155*	Temperature	.129	15
RM 35	1974	Temperature, Turbidity, Conductivity and HCO_3.	.666*	Turbidity	.001	20
EC 4	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, and Light (F.C.).	.770	Turbidity	.001	13
			.902	Turbidity, HCO_3	.003	13
			.921*	Temperature, Turbidity, HCO_3	.001	13
LNFK 1	1974	Temperature, TOC[1], Ortho PO_4, NO_3, Turbidity, SO_4, Fe, Si, and HCO_3.	.857	Turbidity	.001	13
			.893	NO_3, Turbidity	.001	13
All stations	1972	Temperature, Conductivity, HCO_3, Turbidity, Zooplankton, NO_3, and Si.	.392	UMHOS	.009	15
			.476*	UMHOS, Si	.075	15

[1]TOC - Total Organic Carbon

Table 30. The relationship of bluegreens to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
RM 3	1972	Temperature, Turbidity, Conductivity and HCO_3.	.255*	HCO_3	.037	16
RM 3	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3 and Light.	.267	Temperature	.032	16
			.401	Temperature and Conductivity	.027	16
RM 19	1972	Temperature, Turbidity, Conductivity, and HCO_3.	.330*	Conductivity	.039	12
RM 19	1973	Temperature, Turbidity, Conductivity, and HCO_3.	.444	Temperature	.001	32
			.585*	Temperature, Turbidity	.001	32
RM 19	1974	Temperature, Turbidity, Conductivity, and HCO_3.	.212*	Conductivity	.008	31
RM 35	1972	Temperature, Conductivity and HCO_3.	.296	Temperature	.042	13
RM 35	1973	Temperature, Turbidity and HCO_3.	.565	Temperature	.001	15
			.687	Temperature, Turbidity	.001	15
			.809*	Temperature, Turbidity, HCO_3	.001	15
EC 4	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, and Light	.461	Temperature	.008	13
			.668*	Temperature, Zooplankton	.007	13
All Stations	1972	Temperature, Conductivity, HCO_3, Turbidity, Zooplankton, NO_3 and Si.	.556	Zooplankton	.001	15
			.765	Zooplankton, HCO_3	.001	15
			.826*	Zooplankton, HCO_3, NO_3	.001	15

Table 31. The relationship of algal productivity to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Selected Variables	Probability of Greater "F"	d.f.
RM 3	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, Light (F.C.), Ortho PO_4, and NO_3.	.459	Zooplankton	.044	8
RM 3	1973	Temperature, Zooplankton, Turbidity, Conductivity, HCO_3, and Light (F.C.)	.425*	Zooplankton	.008	14
RM 3	1974	Temperature, Turbidity, Ortho PO_4, NO_3, Conductivity, HCO_3 and Light (F.C.)	.168	HCO_3	.028	27
EC 4	1974	Temperature, Ortho PO_4, NO_3, Zooplankton, Turbidity, Conductivity, HCO_3, and Light (F.C.).	.223	HCO_3	.140	10

Table 32. The relationship of total bacteria to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS). (continued)

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
EC 4	1974	Zooplankton, Ortho PO_4, NO_3, Conductivity, Turbidity, and Total Algae.	.236	Ortho PO_4	.084	12
			.395*	Ortho PO_4, NO_3	.080	12
All Stations	1972	Zooplankton, Total Algae, POC[1], NO_3, Conductivity, and Turbidity.	.770	Total Algae	.001	14
			.825	Total Algae, POC	.001	14
			.847	Zooplankton, Total Algae, Conductivity	.001	14
All Stations	1973	Total Algae, Bluegreen Algae, HCO_3, Percent O_2 Saturation, Temperature, TOC, POC, Ortho PO_4, NO_3, Turbidity, Conductivity and Diatoms.	.500	Bluegreen Algae	.015	10
			.638	Bluegreen Algae, Diatoms	.017	10
			.745	Bluegreen Algae, Diatoms, Total Algae	.018	10
			.972*	Bluegreen Algae, Diatoms, Total Algae, HCO_3	.001	10
All Stations	1973	HCO_3, Percent O_2 Saturation, Temperature, Turbidity and Conductivity.	.106	Turbidity	.047	36
			.148	Turbidity, Conductivity	.064	36
All Stations	1974	Zooplankton, Total Algae, POC, Ortho PO_4, NO_3, TOC[2], Conductivity and Turbidity.	.138	Turbidity	.171	14
			.427	POC, TOC	.035	14
			.574*	Total Algae, POC, TOC	.020	14
All Stations	1974	HCO_3, Percent O_2 Saturation, Temperature, Turbidity, and Conductivity.	.069	Conductivity	.010	94
			.103	Percent O_2 Saturation, Conductivity	.007	94
			.130*	Percent O_2 Saturation, Turbidity, Conductivity	.006	94
All Stations	1974	Total Algae, Bluegreen Algae, HCO_3, Percent O_2 Saturation, Temperature, TOC, POC, Ortho PO_4, NO_3, Zooplankton, Conductivity and Diatoms.	.138	Turbidity	.170	14
			.427	TOC, POC	.035	14
			.600*	TOC, POC, Bluegreen Algae	.015	14

[1]POC = Persulfate Oxidizable Carbon
[2]TOC = Total Organic Carbon

Table 33. The relationship of coliform bacteria to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Variable (s) Selected	Probability of Greater "F"	d.f.
RM 3	1974	Total Algae, Zooplankton, NO_3, POC[1], Ortho PO_4, Turbidity, HCO_3 and Conductivity	.408	NO_3	.002	21
			.512*	NO_3, Turbidity	.001	21
RM 3	1973	Total Algae, Zooplankton, Turbidity, HCO_3, and Conductivity.	.291	Turbidity	.210	6
EC 4	1973	Total Algae, Zooplankton, NO_3, POC, Ortho PO_4, Turbidity and HCO_3.	.846	HCO_3	.001	8
			.896	Total Algae, HCO_3	.002	8
			.975	Total Algae, POC, HCO_3	.001	8
			.986	Total Algae, POC, Ortho PO_4, HCO_3	.002	8
			.993*	NO_3, POC, Ortho PO_4, Turbidity, HCO_3	.002	8
All Stations	1972	Total Algae, Zooplankton, NO_3, POC, Turbidity, HCO_3, and Conductivity.	.218*	Conductivity	.004	13
All Stations	1974	Total Algae, Zooplankton, NO_3, Ortho PO_4, TOC[2], POC, Turbidity, HCO_3 and Conductivity.	.287	POC	.038	14
			.435*	POC, Turbidity	.032	14
				POC, Turbidity, Conductivity	.021	14

[1]POC = Persulfate Oxidizable Carbon
[2]TOC = Total Organic Carbon

Table 34. The relationship of zooplankton to limnological variables selected by a stepwise multiple linear regression best-fit analysis (SAS).

Station	Time	Model Variables	R^2	Selected Variables	Probability of Greater "F"	d.f.
RM 3	1972	Temperature, Turbidity, Conductivity and HCO_3.	.462*	HCO_3	.030	9
RM 3	1973	Temperature, Turbidity, Conductivity, Ortho PO_4, NO_3, HCO_3, and Light (F.C.)	.284*	Ortho PO_4	.072	11
RM 3	1974	Temperature, Turbidity, Conductivity, HCO_3 and Light (F.C.).	.424 .576*	Temperature Temperature, HCO_3	.001 .001	21 21
RM 19	1973	Temperature, Turbidity, Conductivity and HCO_3.	.183 .389*	Temperature Temperature, Turbidity	.095 .040	15 15
RM 19	1974	Temperature, Turbidity, Conductivity and HCO_3.	.810 .882	Temperature Temperature, HCO_3	.001 .001	9 9
RM 35	1973	Temperature, Turbidity, and HCO_3.	.576*	Temperature	.017	8
EC 4	1973	Temperature, Turbidity, Conductivity, HCO_3, and Light (F.C.).	.310	Light (F.C.)	.030	14
EC 4	1974	Temperature, Turbidity, Ortho PO_4, NO_3, Conductivity, and HCO_3.	.226	Temperature	.038	18
All Stations	1973	Temperature, Ortho PO_4, NO_3, Turbidity, Conductivity, HCO_3, and Light (F.C.)	.146 .269	Light Light, Ortho PO_4	.350 .014	29 29

CONCLUSIONS

1. Dworshak is a coldwater reservoir with a mean temperature ~46 F.
2. Thermal stratification shows a steep gradient near surface at all sites in the reservoir. An exceptionally stable water column resulted with little interaction between vertical layers from May through August.
3. Near-surface withdrawal of water from Dworshak Reservoir with selector gate operation permitted summer matching of downstream temperatures but lowered the summer-fall mean temperatures of the surface layer in the lower reservoir, i.e. near surface withdrawal resulted in a less stable water column more susceptible to mixing.
4. Shoreline sources, primarily from slumping and wave action were the major sources of turbidity to the water column.
5. Oxygen depletion to zero occurred in deepwaters one year after filling, attributed primarily to decomposition of leached soluble organic matter from newly submerged soils and vegetation.
6. Dworshak's trend toward oligotrophy is indicated by relatively high, increasing deepwater oxygen levels in 1974.
7. Nitrogen limitation to algal production was probable in the first year after filling, 1972, and appeared to be sporadically limiting along with phosphorous in 1973 and 1974. In future years, Dworshak production will be severely nutrient-limited.

8. In 1974, late winter drawdown and rains resulted in high surface turbidity which retarded onset of algal and zooplankton production by 6-7 weeks. Low surface water temperatures later in mid-summer apparently held down algal production once initiated.

9. Onset of zooplankton production was also severely set back in time as a result of spring 1974 high turbidity.

10. Within two years after filling, phytoplankton and zooplankton production declined to approximately 30-40% of initial levels.

11. At the end of this study neither plankton community production nor composition had stabilized. It is projected that production will stabilize ~20% lower than the 1974 level; phytoplankton diversity will continue to slowly increase to a point at least 50% greater than the 1974 diversity.

RECOMMENDATIONS

1. An analytical heat budget should be calculated each future year, detailing sources and losses of heat to and from the reservoir. These accurate estimates of heat input could then be compared with production variations from year to year in an effort to further delineate the role of temperature in controlling production. Variations in heat content with different operational patterns in a given year could then be analysed after correction for varying heat input.
2. A turbidity/suspended solids budget should be prepared from estimates of tributary inputs, shoreline inputs, and reservoir outflow. With documentation of sources and reservoir turbidity levels under different dam management options, future reservoir turbidity resulting from future operational schemes might be predicted.
3. Hypolimnial oxygen deficits should be determined at RM 3 and off future recreational areas in late summer of each year. Two O_2 profiles, one in early July and one in early September, would suffice from each area. The resulting oxygen consumption rate for each summer would be a concise estimate of organic decomposition, reflecting overall organic production and/or release and its subsequent breakdown, thus providing a barometer of the reservoirs change rate. The water columns off RM 3 and recreational sites will be the first areas of the reservoir to show change from the near "baseline" conditions represented by 1974.

4. Since nutrient limitation in Dworshak Reservoir was evident sporadically in 1972-74, and since overall nutrient levels have been declining since the reservoir was first filled, a year-round nutrient budget detailing nutrient inputs to specific water layers is required to define the nutrient residence times and fates within the reservoir.

5. Future log ponding in Dworshak Reservoir should be accompanied by nutrient analyses of the water column beneath log rafts to ascertain the feasibility of such nutrient addition stimulating epilimnial production, especially in low volume bays. The increase in fish production could be substantial.

6. In view of the pronounced oligotrophy of Dworshak Reservoir and the resulting low fish production mid-depth discharge of treated, sterilized sewage wastes from recreation areas remains a possibility to stimulate production in certain embayments.

7. Various regimes of selector gate operation need to be related to patterns of organic production through the summer-fall high production period. Since selector gate operation to maximize downstream temperatures results in a cooler, hence more unstable epilimnion in the fall, might not the resulting early recharge of deepwater nutrients to the surface water stimulate early fall production? In fact, the mixis timing in 1974 was 3 weeks earlier than in the other two years and a major fall plankton pulse did occur. Cause and effect need to be delineated.

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PHYSICAL AND CHEMICAL CHARACTERISTICS OF LOG LEACHATES FROM SELECTED CONIFEROUS WOOD AND THEIR EFFECT ON THE NATURAL ALGAL POPULATIONS OF DWORSHAK RESERVOIR, IDAHO

Part 2 of

EARLY LIMNOLOGY OF DWORSHAK RESERVOIR

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TABLE OF CONTENTS

Page

LIST OF TABLES 2-iii

LIST OF FIGURES. 2-iv

ABSTRACT 2-vi

INTRODUCTION 2-1

METHODS 2-4

Experimental Leaching 2-4
In-situ Bioassay. 2-7
Analysis of Data. 2-8

RESULTS AND DISCUSSION 2-10

Leaching Experiments. 2-10
Color - Tannin-like Substances 2-10
pH - CO_2 - Alkalinity. 2-16
Conductivity 2-21
Bacteria 2-23
BOD - COD. 2-23
Phosphate. 2-29
Nitrate. 2-30
Field Application 2-33
In-situ Bioassay. 2-36

CONCLUSIONS 2-51

LITERATURE CITED 2-52

LIST OF TABLES

Table		Page
1	Physical measurements of log sections used in leaching experiments, 1974-1975	2-5
2	Chemical characteristics of water containing selected coniferous tree species (crosscut ends unsealed) floating half submerged in 1110 liters of water for two consecutive thirty day leaching periods, 1974-1975	2-11
3	Chemical characteristics of water containing selected coniferous tree species (crosscut ends sealed) floating half submerged in 1110 liters of water for two consecutive thirty day leaching periods, 1975	2-12
4	Biochemical oxygen demand (BOD_5), COD, and BOD_5:COD values for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-28
5	Addition rates of leachates produced by a hypothetical log raft of 100,000 m^2, all bark intact, floating half submerged for 1 day and 1 month	2-35
6	Initial nutrient levels of Dworshak Reservoir water prior to each bioassay (1-6), conducted May-October, 1974; and nutrient levels contributed by the addition of log leachates to 40 liters of Dworshak Reservoir water in polyethylene bags, 1974	2-37

LIST OF FIGURES

Figure		Page
1	Dworshak Reservoir study area and major tributaries	2-2
2	Diagram of polyethylene enclosures and anchored buoy used in bioassays conducted between May and October, 1974, Dworshak Reservoir, Idaho	2-9
3	Water color development (measured against platinum-cobalt standards) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-13
4	Tannin-like substances (expressed as grams/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-15
5	pH values for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-17
6	Carbon dioxide (expressed as g/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-19
7	Methyl-orange alkalinity (expressed as grams ($CaCO_3$/m^2 submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-20
8	Specific conductance (umhos) for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-22
9	Total coliform bacteria (cells/1) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day leaching periods, 1974-1975	2-24
10	Biochemical oxygen demand (BOD_5) values (expressed as grams O_2/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-25
11	Chemical oxygen demand (COD) values (expressed as grams O_2/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975	2-27

Figure | Page

12 Phosphates (expressed as g/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975 2-31

13 Nitrate-nitrogen (expressed as g/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974 2-32

14 Chlorophyll *a* in 8 day bioassays at various concentrations of log leachates in Dworshak Reservoir water, bioassays Nos. 1-3, conducted May 7-June 20, 1974 2-39

15 Algal response (average of treatments) to log leachates in 40 liters of Dworshak Reservoir water. Bioassay No. 4 conducted July 1-5, 1974 2-40

16 Algal cell counts and chlorophyll *a* on the 5th day of bioassay No. 4, conducted on Dworshak Reservoir, July 1-5, 1974 2-41

17 Algal response (average of treatments) to log leachate in 40 liters of Dworshak Reservoir water. Bioassay No. 5 conducted August 23-27, 1974 2-43

18 Algal and bacterial cell counts on the 5th day of bioassay No. 5 conducted on Dworshak Reservoir, August 23-27, 1974 2-44

19 Algal response to treatments for duplicate bioassays conducted at Dworshak Reservoir. Bioassay No. 6, October 14-18, 1974 2-46

20 Treatment response (duplicates combined) for Dinobryon on the 5th day of bioassay No. 6 conducted at Dworshak Reservoir, October 14-18, 1974 2-48

21 Generalized comparison of algal response to log leachates, control, and the reservoir environment over a 5 day period. Dworshak Reservoir, 1974 2-49

ABSTRACT

With the filling of Dworshak Reservoir in October, 1971, a large portion of the 185 million board feet of timber in the reservoir basin was subjected to leaching. This study determined the leaching rates of this wood, and effects of leachates on the reservoir water quality and natural algal populations.

Most soluble organic matter leached from logs comes from woody tissues rather than bark. These soluble organics increased the BOD_5 and COD of the holding water. In 30 days of experimental leaching, BOD_5 values reached a high of approximately 27 g/m^2 submerged log surface area and COD measurements exceeded 200 g/m^2. These results when expanded to a log raft of 100,000 square meters submerged surface area would yield 181 kg of COD per day and 54 kg of BOD per day. It is not believed that the leaching of these substances would have a detrimental effect on the reservoir's water quality due to the large reservoir volume. Additional parameters measured included: color, methyl-orange alkalinity, total coliform bacteria, pH, specific conductance, nitrate-nitrogen, and orthophosphate.

Nitrate-nitrogen and orthophosphate were high in log leachates. In 30 days of leaching, logs contributed 0.10 g/m^2 of nitrate-nitrogen and 0.55 g/m^2 of orthophosphate.

During the spring and fall of 1974, a total of 6 in-situ bioassays were conducted on Dworshak Reservoir. A range of log leachate concentrations was added to 40 liters of reservoir water and incubated from 5 to 8 days in polyethylene bags. Results showed that log leachates generally increased algal production, though a toxic response was noted in some algal genera.

INTRODUCTION

Dworshak Reservoir is located on the North Fork of the Clearwater River in Northern Idaho. The 85 kilometer, 6900 hectare, flood storage reservoir began filling in October, 1971, but was not completed by the U.S. Army Corps of Engineers until 1972 (Figure 1).

A survey conducted in 1960 by the U.S. Forest Service estimated a total of 185 million board feet (MBF) of saw and pole timber below the 484 meter (mean sea level) high water contour. Of this 185 MBF, approximately 58 MBF were left below the 436 meter contour as the reservoir began filling. The remaining 127 MBF was either cut from the variable shoreline between the 485 meter and 436 meter contours or selectively harvested from below the 436 meter contour before the reservoir began filling. A considerable portion of this timber remained floating in the reservoir for up to two years prior to removal.

This study is a portion of a larger study, "Early Limnology of Dworshak Reservoir," funded by the U.S. Army Corps of Engineers Contract Number DACW 68-72-C-0142. The purpose of this sub project was to:

1) Assess leachates of water quality importance contributed by the coniferous tree species common to Dworshak Reservoir.
2) Estimate plant nutrients contributed by the floating logs.
3) Experimentally measure the impact of log leachates on the reservoir's natural algal populations.

Recent studies concerning the impact of wood and bark leachates on the aquatic environment indicate that these pollutants have a direct and adverse effect on water quality (Graham and Schaumburg 1969; Sproul and

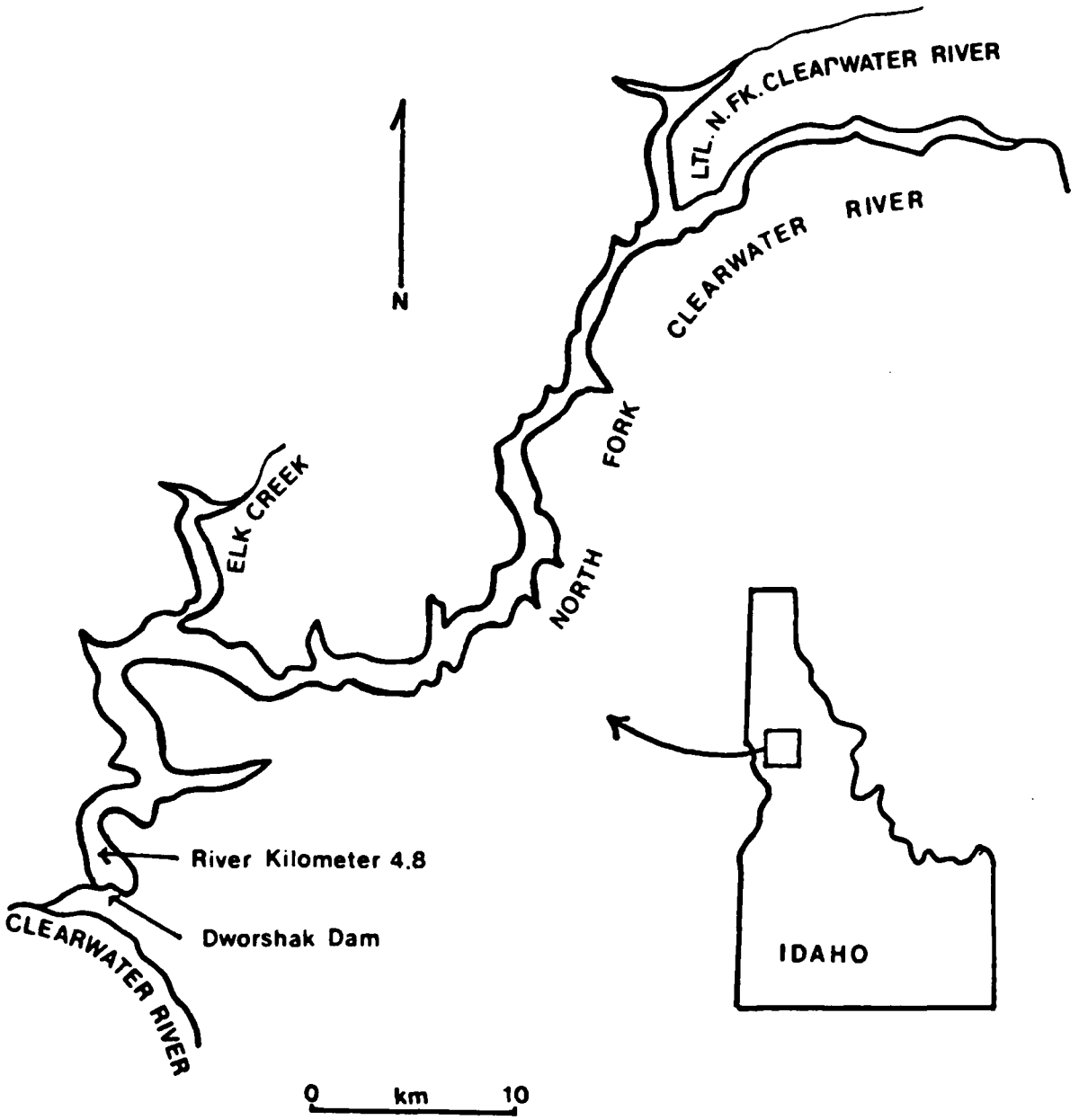

Figure 1. Dworshak Reservoir study area and major tributaries.

Sharpe 1968; Hoffbuhr, Blanton and Schaumburg 1971; Schaumburg 1972). Chemical parameters and leaching rates were emphasized in all studies. Five day biochemical oxygen demand (BOD_5) and chemical oxygen demand (COD) of both wood and bark leachates were found to have the greatest impact on water quality. Studies of leachate toxicities were limited to effects on salmon and trout fry and egg survival (Servizi, Martens and Gordon 1971; Schaumburg and Atkinson 1970). Little work has been done on the effects of log leachates on primary production.

METHODS

Experimental Leaching

The purpose of the experimental leaching was: 1) to assess the chemical and physical characteristics of leachates contributed by coniferous tree species common to Dworshak Reservoir, 2) to determine the rate of release of these chemical pollutants into the holding water, and 3) to estimate plant nutrients contributed by the floating logs.

We selected four coniferous tree species for these experiments: Douglas fir, Pseudostuga menziesii; grand fir, Abies grandis; ponderosa pine, Pinus ponderosa; and western redcedar, Thuja plicata. These species comprise 83 percent of the volume (board feet) of all coniferous tree species present in the reservoir basin. All logs were taken from a location approximately 15 miles north of the reservoir. The site selected was similar to the reservoir area in terms of habitat type, soil types, and topography. After felling, we removed one 120 cm (4 ft) section from the base of each tree and transported it to the University of Idaho Fisheries Laboratory where each log was cut into 30.5 cm (1 ft) lengths and labeled as to species. Physical dimensions and age were determined (Table 1).

In order to expand the experimental findings in this study to the actual reservoir situation, it was necessary to determine the differential leaching rates between the 30 cm (1 ft) log sections used in this experiment and a full sized log. This was accomplished in two separate experiments. First, we selected 8 logs: 3 Douglas fir, 2 grand fir, 2 ponderosa pine, and 1 western redcedar. The bark and crosscut ends on these logs were left unsealed. We leached this set of logs in water for 30 days, then changed

Table 1. Physical measurements of log sections used in leaching experiments, 1974-1975.

Species	Number of Log Replicates	Length (cm)	Avg. Diameter (cm)	Total* Board Feet (bd ft)	Age (yrs)	Percent Sapwood (%)	Bark Thickness (cm)
			UNSEALED LOGS				
Douglas fir	3	30.5	26.0	2.5	33	40	1.3
		30.5	26.0	2.5	33	40	1.3
		30.5	26.0	2.5	33	40	1.3
Grand fir	2	30.5	24.6	2.5	33	79	1.3
		30.5	24.1	2.5	33	79	1.3
Ponderosa pine	2	30.5	25.4	2.5	27	96	1.9
		30.5	24.8	2.5	27	96	1.9
Western redcedar	1	30.5	29.2	5.0	103	30	1.5
				Total 22.5 bd ft		63% (Avg)	
			SEALED LOGS				
Douglas fir	3	30.5	22.2	2.5	32	63	1.3
		30.5	21.0	2.5	33	63	1.3
		30.5	21.6	2.5	34	63	1.3
Grand fir	2	30.5	21.6	2.5	32	78	1.3
		30.5	22.9	2.5	34	77	1.3
Ponderosa pine	2	30.5	16.5	1.3	32	98	1.9
		30.5	15.2	1.3	32	98	1.9
Western redcedar	1	30.5	21.6	2.5	62	56	1.3
				Total 17.6 bd ft		75% (Avg)	

*Approximate volumes according to Schribner Decimal C Log Rule (Dilworth 1970).

REMARKS: The total exposed wood and bark on the unsealed logs was 25,028 cm^2; the total exposed bark was 16,500 cm^2.

The total area of wood and bark on the sealed logs was 20,416 cm^2 and 13,000 cm^2 with the ends sealed (bark only exposed).

the water in the test tanks. The log sections leached for an additional 30 days. This method permitted separation of longitudinal from radial leaching of each log section.

The second experiment was conducted with a similar set of logs but each log had the crosscut end sealed with paraffin. These logs were also leached for two consecutive 30 day periods. This method allowed only for radial leaching through the bark. By using the data from each experiment in a modification of the formula set forth by Schaumburg (1972), a comparison was made to the actual reservoir situation.

For the experimental leaching we used two holding tanks (control and experimental) constructed of plywood and coated with fiberglass resin. Each tank had a 1110 liter capacity. We filled each tank with distilled water and enough tap water (about 110 liters) to raise the conductivity of the holding water to about 25 umhos. This value approximates the mean annual conductivity of Dworshak Reservoir. Water temperature for both experiments was maintained at 15 C in a temperature controlled room.

Water samples were taken at 5 day intervals for both experiments and we analyzed them for: pH, color, oxygen, carbon dioxide, methyl-orange alkalinity, conductivity, total coliform bacteria, BOD_5, COD, tannin-like substances, nitrate-nitrogen, and orthophosphate-phosphorus. Prior to the removal of each sample, the water was manually stirred to assure a homogenous mixture. Oxygen, pH, carbon dioxide, alkalinity, conductivity, and BOD were measured immediately after sampling. All other samples were preserved with $HgCl_2$ (40 mg/l) and frozen immediately for later analysis. All water chemical and bacterial analyses were made according to Standard Methods for the Analysis of Water and Wastewater (1971). Coliform bacterial analyses

were conducted by the Millipore membrane filtration technique and incubated at 35 C for 24 hours. Tannin-like substances were determined with a tannic acid standard. We ran orthophosphate-phosphorous using the stannous chloride method and the nitrate-nitrogen analysis using the brucine-sulfanilic acid method. Color measurements were made against a set of platinum-cobalt standards. All results, when applicable, are expressed in grams of leachate per square meter of submerged log surface. We chose this procedure so these data could be compared to previous work and would be more applicable to the reservoir situation.

In-situ Bioassay

The purpose of the in-situ bioassays was to experimentally measure the impact of differing concentrations of log leachates on the natural algal populations of Dworshak Reservoir.

We conducted six 120 to 190 hour in-situ algal bioassays in Dworshak Reservoir between May and October, 1974. The site for the bioassays was the log storage area at River Kilometer 4.8 (Figure 1). Each bioassay consisted of a predetermined leachate inoculant placed in a 40 liter, 2 mil (105 mm thick) polyethylene bag. The leachates used for this experiment were contained in tank water from the second 30 days of the "unsealed logs" leaching experiment. Three to four treatment bags and one control bag were used in each bioassay. The last bioassay conducted October 14-18, 1974, consisted of duplicate sets of treatment and control bags to determine the variability associated with the technique. Incubation periods were limited to 5 to 8 days to minimize the tendency toward eutrophication (Porter 1972).

Each bag was filled with unfiltered reservoir water taken from a depth of 5 meters with an 8 liter stainless steel Kemmerer bottle. In the last three bioassays (nos. 4 through 6) a 5 liter PVC plastic Kemmerer bottle was used instead of the stainless steel bottle to avoid any toxicity associated with the metal container. Concentrations of the leachate in the 40 liters of reservoir water ranged from 0.125 to 2.5 percent. These percentages were calculated to represent concentrations above, below, and equal to the concentrations contributed by the logs floating in the reservoir epilimnion.

Immediately after filling each bag and mixing, a sample was removed for the following analyses: nitrate, orthophosphate, COD, chlorophyll a, algal composition, and algal biomass. The bags were then resuspended at 5 meters from an anchored buoy (Figure 2).

Chlorophyll a was determined by the spectrophotometric method for phytoplankton (Slack, Averett, Greeson and Lipscomb 1973). Algal biomass and composition were analyzed using a Wild inverted microscope and a modified sedimentation technique (Lund, Kipling and LeCren 1958).

Analysis of Data

Differences between sample means were determined using the non-parametric Kruskal-Wallis test for a completely randomized design (Conover 1971). We ran correlations using treatments as the independent variable against the total algal numbers, and total algal numbers for each taxonomic group as the dependent variables. All variables were transformed with a $\text{Log}_{10} + 1$ transformation.

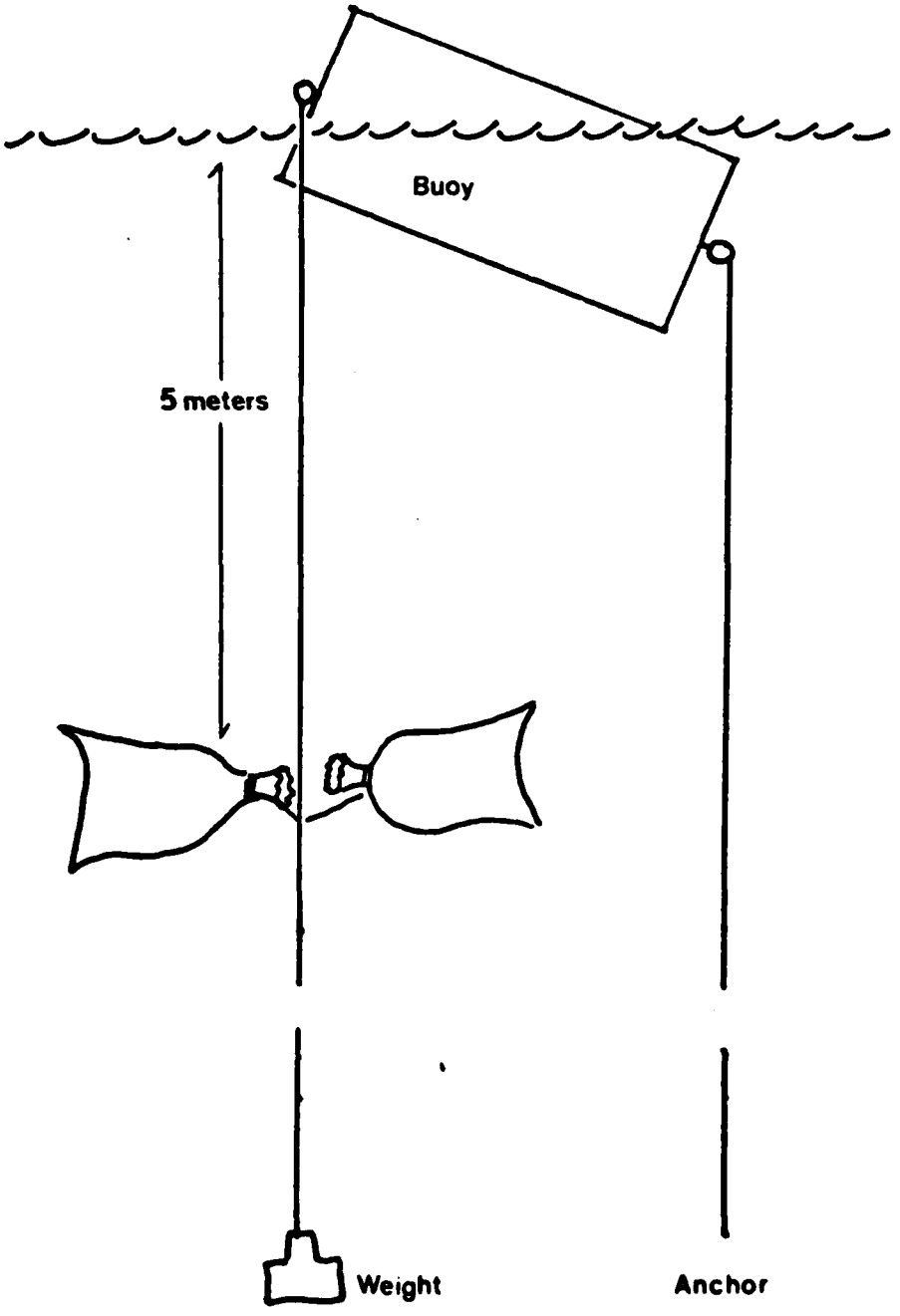

Figure 2. Diagram of polyethylene enclosures and anchored buoy used in bioassays conducted between May and October, 1974, Dworshak Reservoir, Idaho.

RESULTS AND DISCUSSION

Leaching Experiments

All results for the leaching experiment, where applicable, are expressed in grams of pollutant leached per square meter of submerged log surface area (Tables 2 and 3). These values were obtained by multiplying the amount of each parameter in g/l in the test tank by the test tank capacity of 1110 liters, then dividing by the total submerged surface area of all log sections used in the experiment. When the crosscut ends were sealed with paraffin, only the area of the submerged bark was used.

Color - Tannin-like Substances

The most obvious change imparted to the water by floating logs was color. This color was released into the holding water almost immediately. In the first 24 hours of leaching, unsealed logs produced a color value of 30 units (measured against platinum-cobalt standards). After 30 days of leaching these same logs had produced a color value of 150 units. A high of 140 color units was reached in the second 30 days of leaching (Figure 3). A drop to 90 color units on the 60th day of leaching indicated a decrease in the release of color producing substances as well as possible utilization by the bacterial community present.

The log sections sealed with paraffin produced little color in either of the two 30 day leaching periods. Color in neither period exceeded 5 units and remained below 5 units until the last day of leaching in each period.

The color imparted to holding water by floating logs has been attributed to the bark and its high concentrations of water soluble tannins

Table 2. Chemical characteristics of water containing selected coniferous tree species (crosscut ends unsealed) floating half submerged in 1110 liters of water for two consecutive thirty day leaching periods, 1974-1975.

Days of Leaching	pH	Conductivity (umhos)	Total Coliforms (cells/ 100 ml)	Color (color units)	Methyl-orange Alkalinity (g/m^2)*	Carbon Dioxide (g/m^2)*	Tannin-like Substances (g/m^2)*	BOD (g/m^2)*	COD (g/m^2)*	BOD: COD Ratio	PO_4-P (g/m^2)*	NO_3-N (g/m^2)*
Start	7.3	25	0	0	21.3	3.6	0	0.8	0		0	0
5	5.5	29	1700	45	20.0	36.4	18.6	7.8	22.0	.35	.20	0
10	5.1	29	--	120	16.9	41.7	37.3	19.3	82.1	.24	.27	.05
15	5.3	40	6600	100	190.3	112.2	48.0	26.6	95.0	.28	.32	.09
20	5.2	48	6200	110	146.5	113.7	71.3	13.4	117.7	.11	.44	.09
25	5.3	61	9500	120	164.3	120.0	88.8	19.1	152.1	.13	.44	.07
30	4.9	84	13,800	150	202.5	129.6	104.8	22.2	200.5	.11	.55	.10
Second thirty days (logs placed in fresh water)												
Start	7.3	25	0	0	40.0	8.0	0	0.4	0		0	0
35	6.7	25	10	40	40.0	15.1	30.2	2.1	19.6	.11	.02	.01
40	6.6	26	323	50	52.0	30.2	24.0	4.3	38.9	.11	.09	.01
50	6.2	26	1200	90	57.7	31.1	27.5	9.4	57.5	.16	.15	.02
55	5.9	26	5000	140	66.6	32.0	38.2	8.9	105.1	.08	.24	.06
60	5.7	27	9900	90	67.8	34.6	58.6	13.2	109.2	.12	.28	.04

*Results expressed in grams per square meter of submerged surface of wood and bark.

Table 3. Chemical characteristics of water containing selected coniferous tree species (crosscut ends sealed) floating half submerged in 1110 liters of water for two consecutive thirty day leaching periods, 1975.

Days of Leaching	pH	Conductivity (umhos)	Total Coliforms (cells/ 100 ml)	Color (color units)	Methyl-orange Alkalinity (g/m^2)*	Carbon Dioxide (g/m^2)*	Tannin-like Substances (g/m^2)*	BOD (g/m^2)*	COD (g/m^2)*	BOD: COD Ratio	PO_4-P (g/m^2)*	NO_3-N (g/m^2)*
Start	6.2	25	0	0	29.1	5.1	0	1.7	0		0	0
5	5.7	23	500	<5	32.9	13.7	3.4	3.5	10.6	.33	0	0
10	5.5	26	2100	<5	44.5	20.5	6.8	8.2	--	--	0	0
15	5.0	24	1000	<5	53.0	23.9	6.8	9.3	16.6	.56	.03	0
20	5.3	28	1800	<5	47.9	23.9	5.1	9.2	18.6	.49		0
25	4.5	25	520	5	58.1	22.2	6.8	8.8	21.9	.40	.09	0
30	4.5	26	1150	5	61.6	32.5	6.8	13.9	27.2	.51	.12	0
Second thirty days (logs placed in fresh water)												
Start	6.3	24	0	0	53.0	17.1	0	0.3	0		0	0
35	6.0	24	--	<5	61.6	20.5	3.4	2.4	3.3	.73	.05	0
40	--	24	490	<5	65.0	25.7	6.8	2.9	5.3	.55	.09	0
45	5.9	24	1500	<5	70.1	34.2	8.6	3.9	6.6	.59	.10	0
50	5.8	24	420	<5	77.0	37.6	6.8	3.7	13.3	.28	.17	0
55	5.7	24	--	5	83.8	39.3	6.8	5.3	13.9	.38	.19	0
60	5.5	24	5100	5	73.5	41.0	6.8	5.9	16.6	.36	.20	0

*Results expressed in grams per square meter of submerged surface of bark.

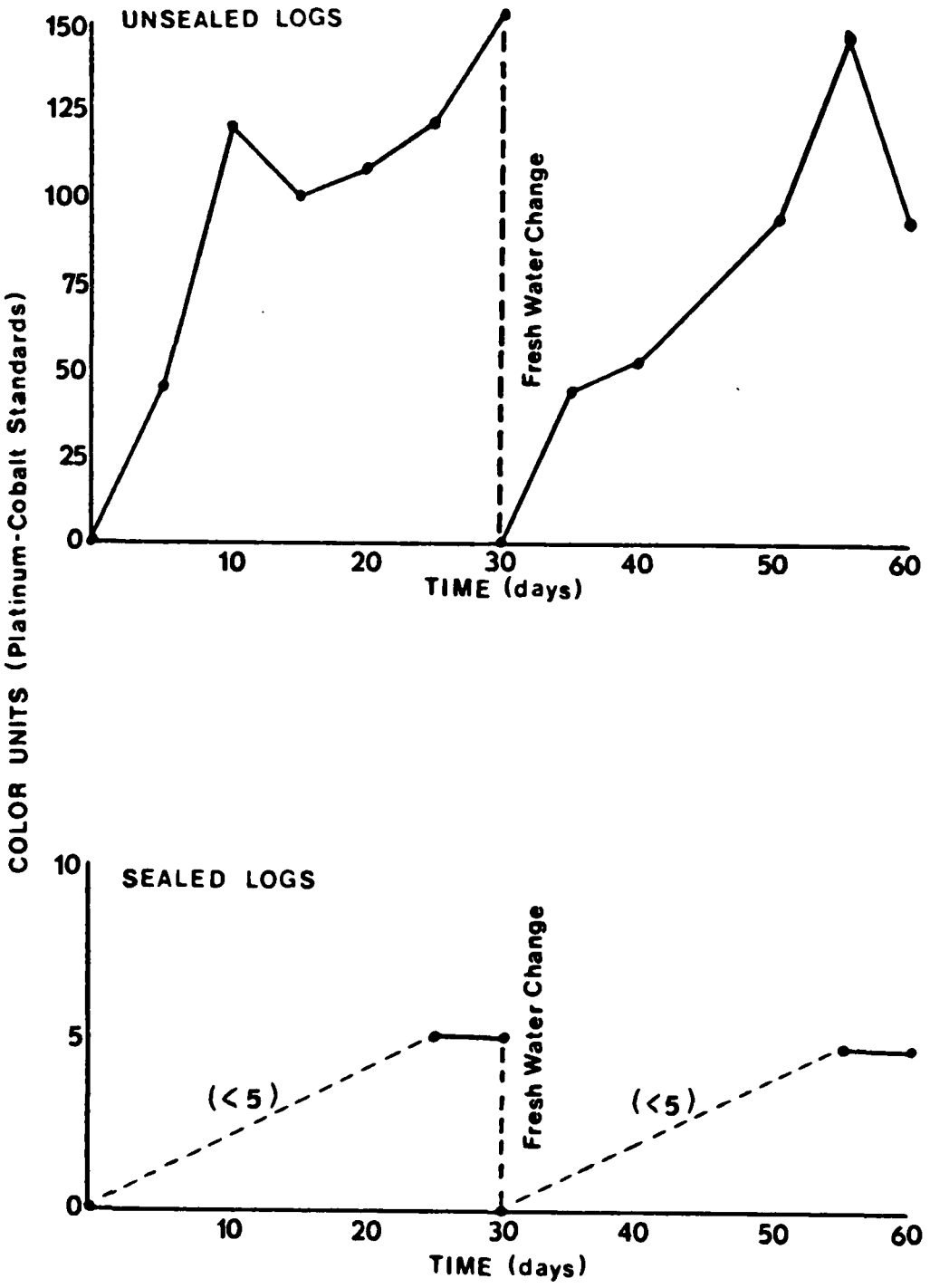

Figure 3. Water color development (measured against platinum-cobalt standards) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

(Graham and Schaumburg 1969; Sproul and Sharpe 1968). Results of these previous experiments produced results contrary to findings of our study. In this experiment, tannin-like substances from unsealed logs did not correspond closely with the color changes in the 60 day leaching period. In the initial 30 day leaching period, these logs produced approximately 105 g/m^2 tannin-like substances (a color value of 150 units). Following the fresh water change, these same logs yielded only 59 g/m^2 tannin but a high color development of 140 units (Figure 4).

If bark is the source of color in holding water, sealing the crosscut ends should cause little change in the color produced. However, sealed logs produced negligible amounts of tannin and color (Figures 3 and 4). These data and the fact that tannin and color do not correspond for the unsealed logs indicate that wood and not bark is the major source of color with the species and test procedures used.

Under normal mixing conditions discoloration of Dworshak Reservoir's water from rafting and storage of logs will be of little importance due to the dilution capacity of the reservoir. In the quiescent conditions produced just beneath a log raft, some discoloration may occur in the first half meter. This color change should not be visible due to the darker underlying waters. Biologically, high concentrations of colored organic matter in water drastically increases the percent total absorption, specifically the ultraviolet, blue, and green wavelengths (Wetzel 1975). The increased absorption of these wavelengths could alter the photosynthetic activities of the photoautotrophs present.

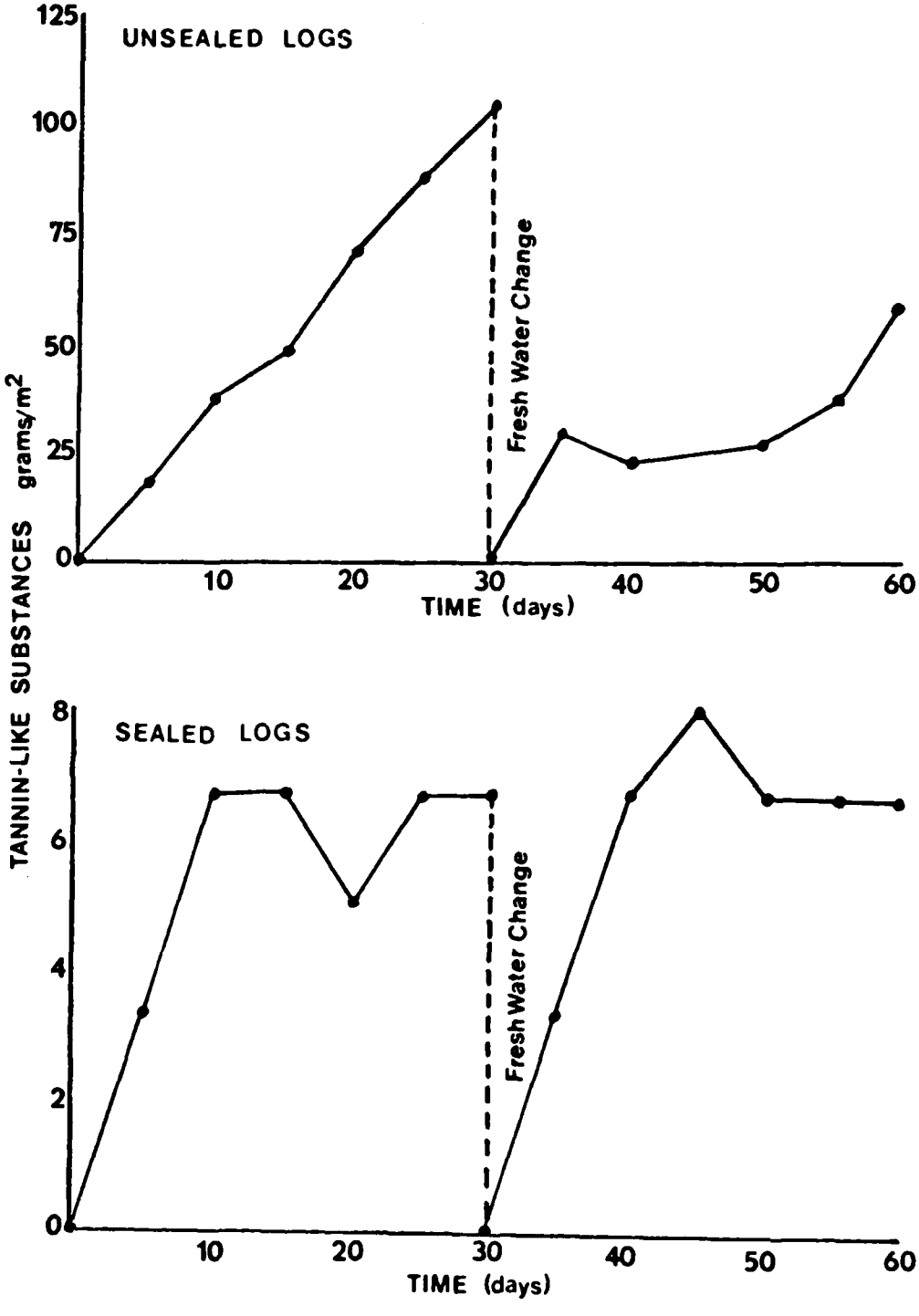

Figure 4. Tannin-like substances (expressed as grams/m^2 of submerged log surface area) in water containing sealed and unsealed logs floating half submerged for two consecutive thirty day periods, 1974-1975.

pH - CO_2 - Alkalinity

The ability of wood and bark to reduce pH of holding water is well documented. Browning (1963) described pH of water-log extracts, including bark, to be as low as 3.5 to 4.5. He gave as a cause, the hydrolysis of acetyl groups to acetic acid in the presence of hot water. Even in cold water some hydrolysis is believed to take place. Sproul and Sharpe (1968) indicated a pH range for bark leachates of 3.5-3.9 and postulated that some of the acidity was due to the presence of acid forming bacteria. Thus, the resulting weak acid solution facilitated further leaching.

The pH measurements showed a gradual decrease for both the sealed and unsealed logs over the 60 day leaching period (Figure 5). This pH decrease was greater for the unsealed logs. In the first 30 days of leaching of unsealed logs pH dropped to 4.90 from an initial 7.35. The second 30 day period resulted in a smaller pH decline from 7.35 to 5.70. The greatest reduction in pH for both 30 day periods was in the first 5 days, when pH decreased at an average rate of approximately 0.30 pH units per day, as opposed to a 0.10 per day decrease in pH for the remainder of each period.

Leaching of the sealed logs resulted in approximately half the reduction in pH that occurred with the unsealed logs for corresponding periods. Again, in the initial 5 days, reduction in pH was the greatest, averaging 0.08 units per day compared to a 0.03 unit per day decrease for the remainder of each period (Figure 5).

These data indicate that both wood and bark contribute substantially to the reduction of pH in holding waters. The rate of reduction for unsealed logs was twice that of sealed logs. The rapid decrease in pH in the first few days of leaching is probably caused by the instantaneous release of

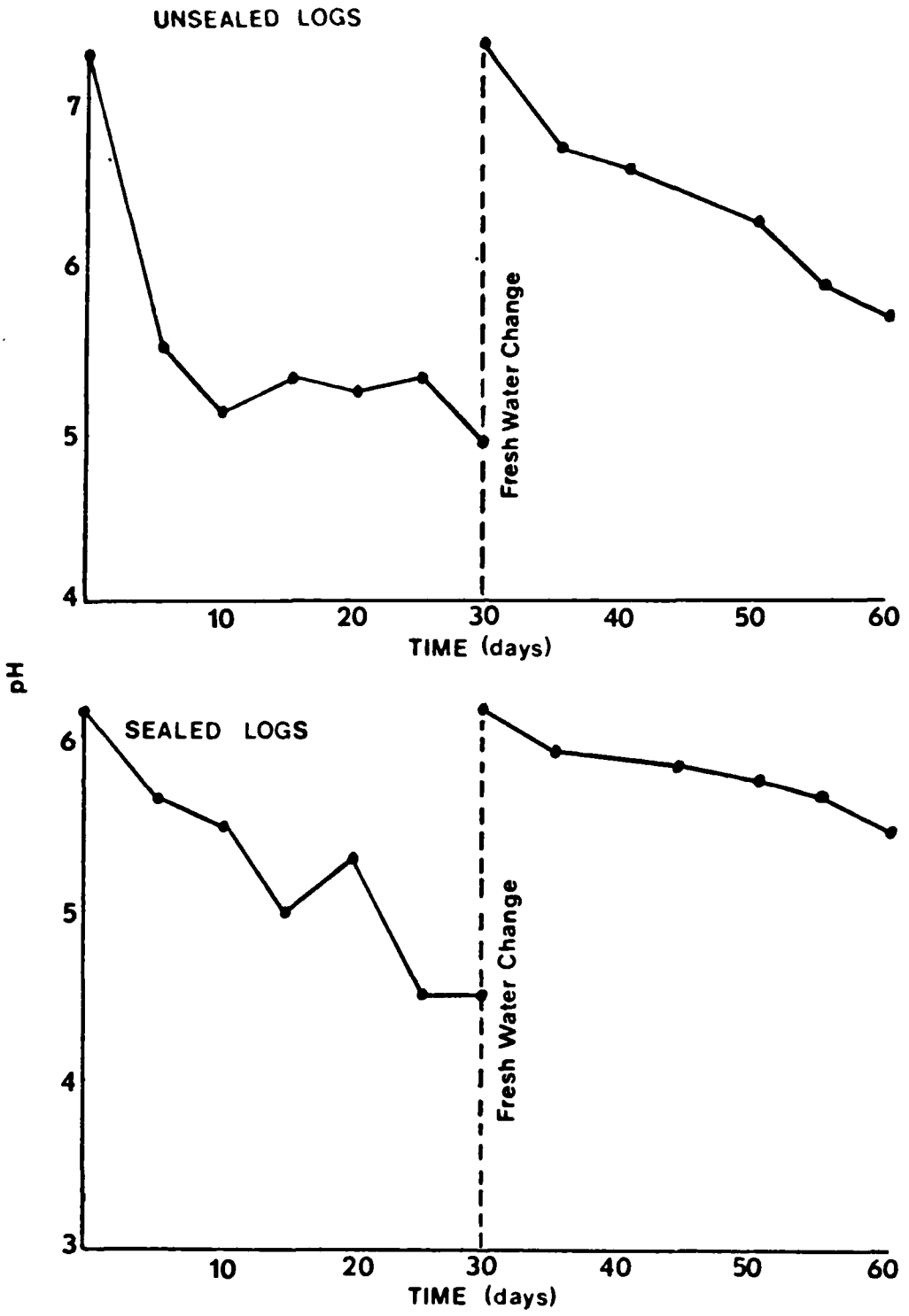

Figure 5. pH values for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

soluble organics when the logs are first placed in fresh water. These organic substances stimulate the growth of bacteria resulting in the production of carbon dioxide which, in conjunction with the formation of acetic acid, helps to maintain a low pH.

The production of carbon dioxide increased for both sealed and unsealed logs in the 60 days of leaching (Figure 6). Leaching of the unsealed logs produced the greatest increase, with approximately 126 g/m^2 generated in the first 30 days of leaching. The evolution of CO_2 for these same logs in the second 30 days reached a maximum of 23 g/m^2. Carbon dioxide increased rapidly between day 10 and 15 in this test (Figure 6). This increase in CO_2 can be attributed to a subsequent increase in bacteria as indicated by the coliform increase from 1700 to 6600 cells/100 ml. Following this increase, CO_2 remained high (114 to 130 g/m^2), as did the coliform counts.

Carbon dioxide generated in the sealed log test was approximately 27 g/m^2 in the first 30 days, starting at 5 g/m^2 and ending at 32 g/m^2. After the fresh water change these logs followed the same trend, producing nearly as much CO_2 as was produced in the first 30 days. A total of approximately 24 g/m^2 was generated in this period.

The much reduced rate of CO_2 production for the unsealed logs in the second 30 day period strongly indicates both the leaching of less biodegradable organic substances and a reduced rate of leaching. By sealing the crosscut log ends, the rate of release of these organics was decreased, thus showing that leaching is primarily a longitudinal process.

Methyl-orange alkalinity increased for sealed and unsealed logs in all leaching periods (Figure 7). A high of 202.5 g/m^2 (as $CaCO_3$) was reached in the first 30 days for the unsealed logs and an additional 28.0 g/m^2 was

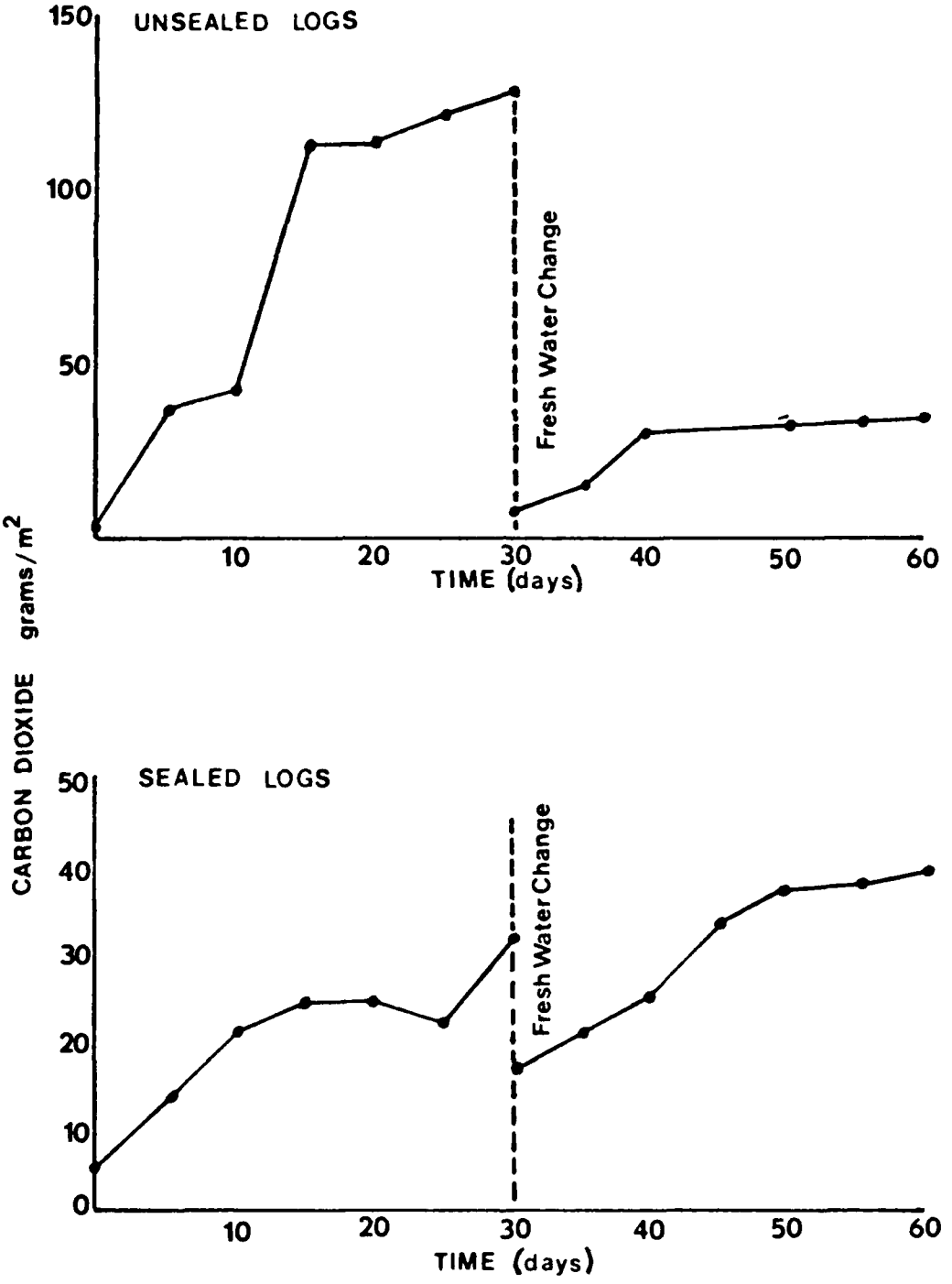

Figure 6. Carbon dioxide (expressed as g/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

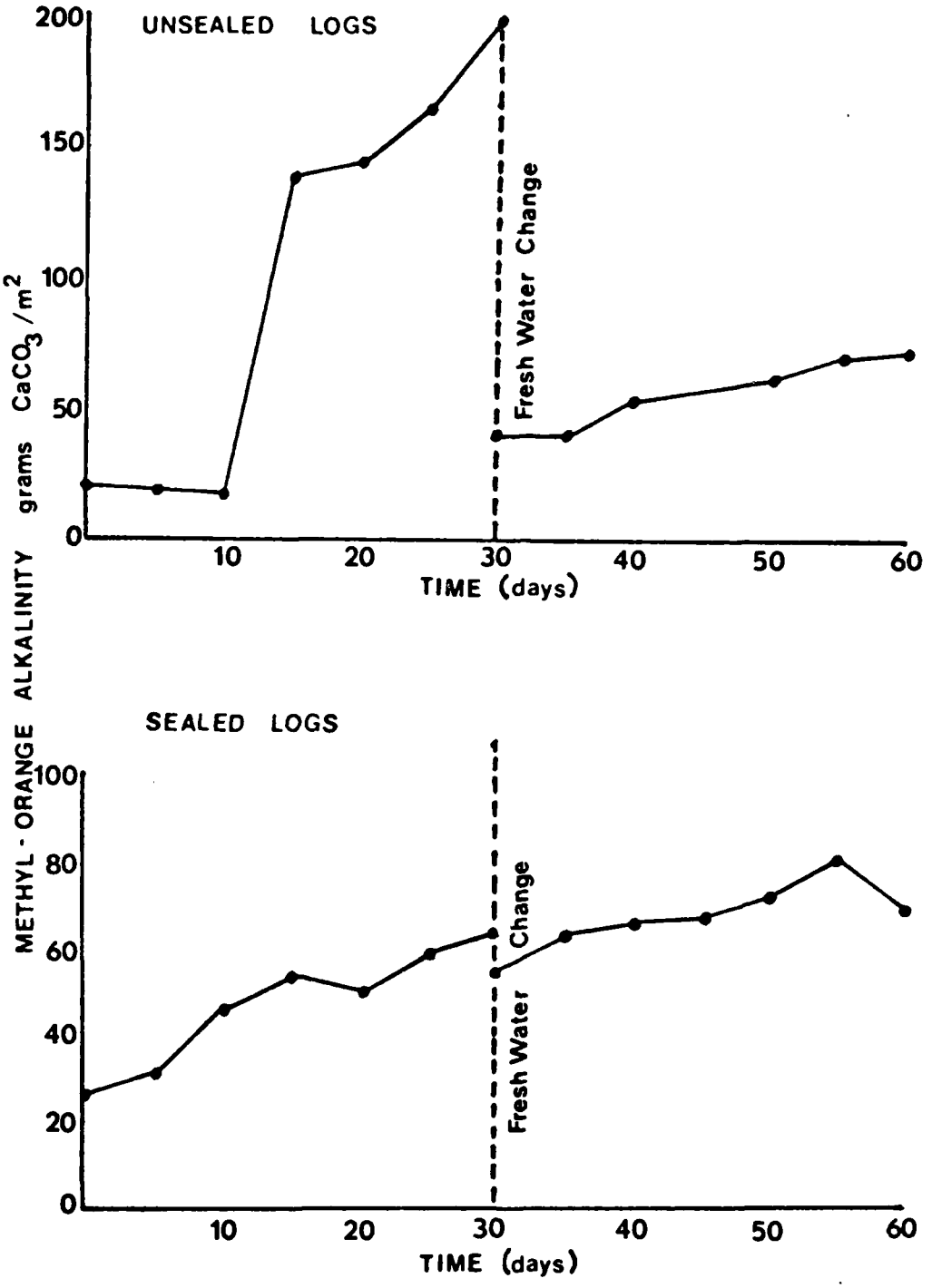

Figure 7. Methyl-orange alkalinity (expressed as grams $(CaCO_3)/m^2$ submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

generated in the second leaching period. A comparison between CO_2 and alkalinity in the first 30 days of unsealed logs shows that with the sudden increase in CO_2, a similar increase is noted in alkalinity. This indicates that the majority of the alkalinity was contributed by CO_2.

Methyl-orange alkalinity for sealed logs increased at approximately 1.5 times as fast in the first 30 day period as in the second 30 days. Production totaled 33.0 and 20.0 g/m^2/30 days respectively (Figure 7). Correction for CO_2 shows that CO_2 accounted for little more than half the alkalinity present.

Both CO_2 and alkalinity are a measure of the potential carbon source for primary production. Abundance of these carbon sources in this experiment suggests a possible enhancement of the reservoir's carbon pool by log leachates.

Conductivity

Only in the first 30 day leaching period for the unsealed logs was there any substantial change in specific conductance of the holding water (Figure 8). During this time the conductivity increased steadily from 25 umhos to 84 umhos, but only an increase of 2 umhos was noted for the same logs in the second 30 day period.

Logs with the ends sealed showed an erratic response in the first leaching period. During this period the conductance fluctuated between 23 and 28 umhos, with a mean value of 25.3 umhos. The second 30 day leaching of these same logs produced no changes, remaining constant at 24 umhos for the entire period.

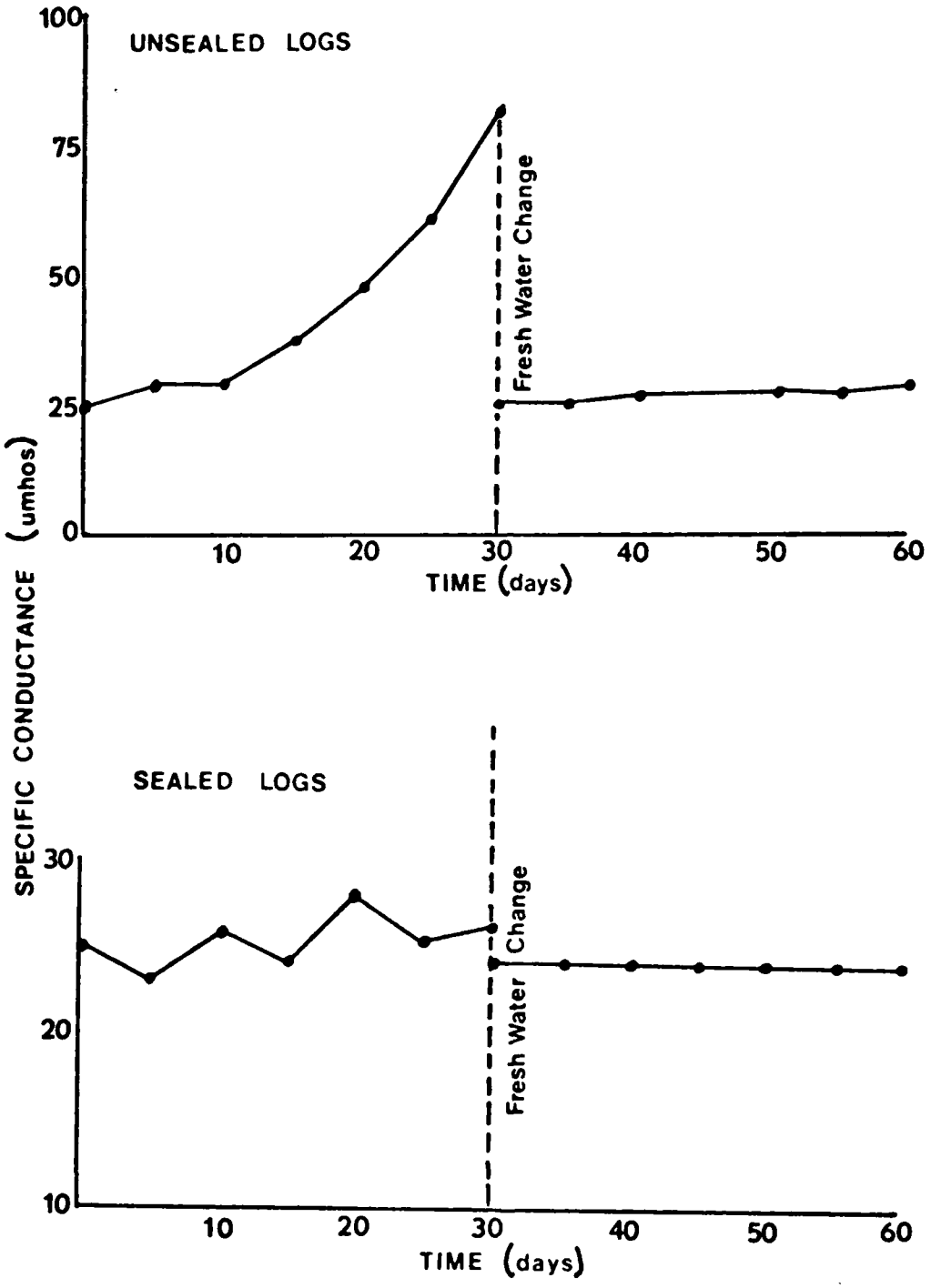

Figure 8. Specific conductance (umhos) for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

Bacteria

Log leachates appear to be an excellent medium for bacterial growth. Total coliform bacteria counts for the unsealed logs increased steadily throughout the 60 day leaching period, ending at a high of approximately 14,000 cells/100 ml in the first 30 days and approximately 9,900 cells/100 ml in the second 30 days (Figure 9).

Total coliform bacteria counts for the sealed logs were less than those of the unsealed logs. A high of 5,100 cells/100 ml was reached on day 60, and only once exceeded 2,000 cells/100 ml prior to this day.

The difference between coliform counts for the sealed and unsealed logs can be explained by the difference in the two leachates as an organic carbon source. The unsealed logs produced approximately 5 times as much organic carbon as did the sealed logs. For both experiments the increase in bacterial numbers closely followed the increase in organic carbon.

BOD - COD

Biochemical oxygen demand and COD measurements were taken on the log leachates in order to evaluate the nature and amount of water soluble substances which are leached from coniferous woods. BOD measures the oxygen required to biologically oxidize an organic substance. COD measures all constituents which can be chemically oxidized.

BOD values for unsealed logs were higher than those for the sealed logs (Figure 10). A high of 26.6 g/m^2 was attained after 15 days of leaching the unsealed logs in the first 30 day period. This compares to 9.3 g/m^2 in the same time period for sealed logs which attained a high of only 14 g/m^2 in 60 days of leaching. Reduced BOD values for sealed logs indicate that the woody tissues contribute the majority of the BOD exerting substances.

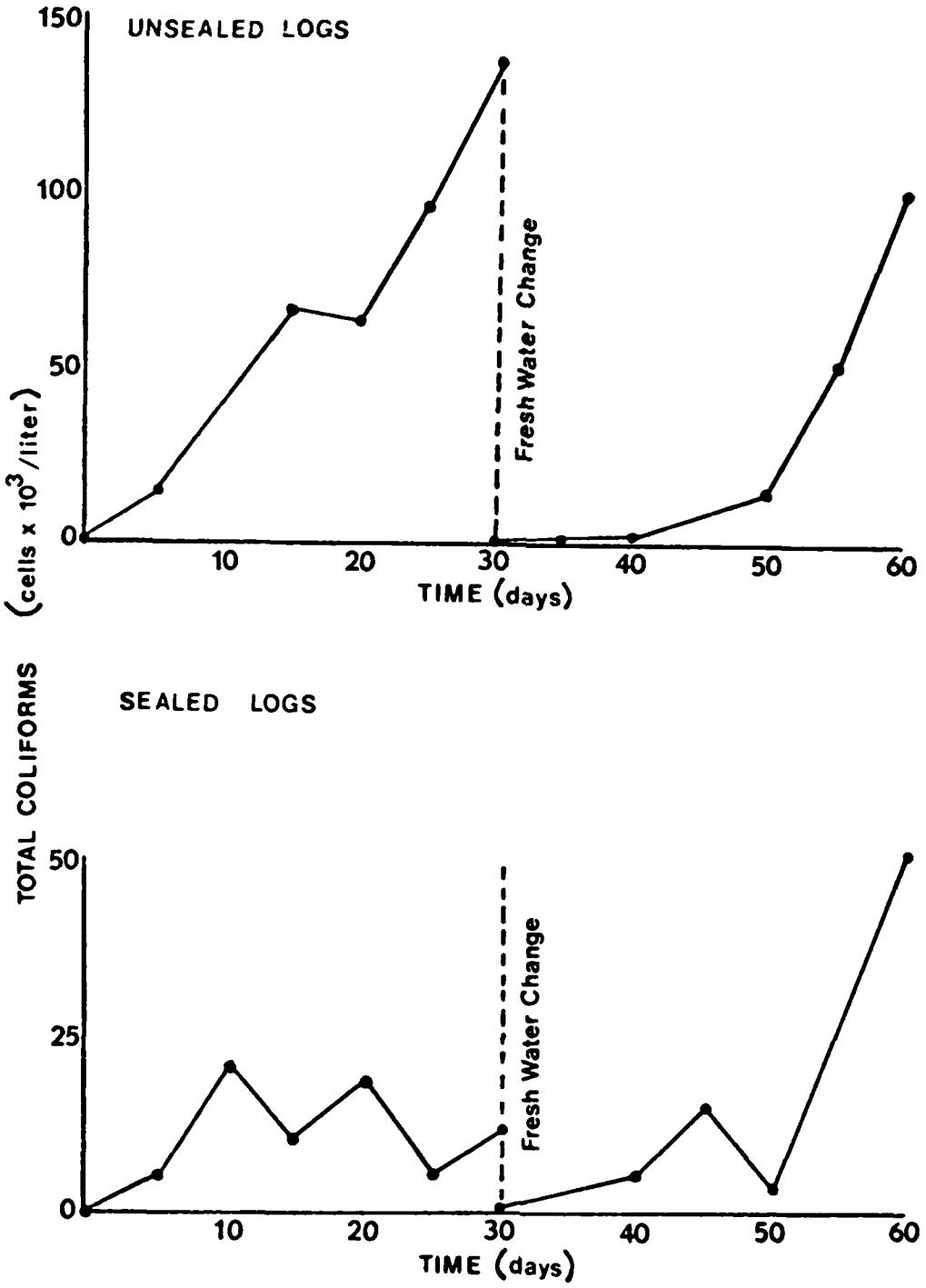

Figure 9. Total coliform bacteria (cells/1) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day leaching periods, 1974-1975.

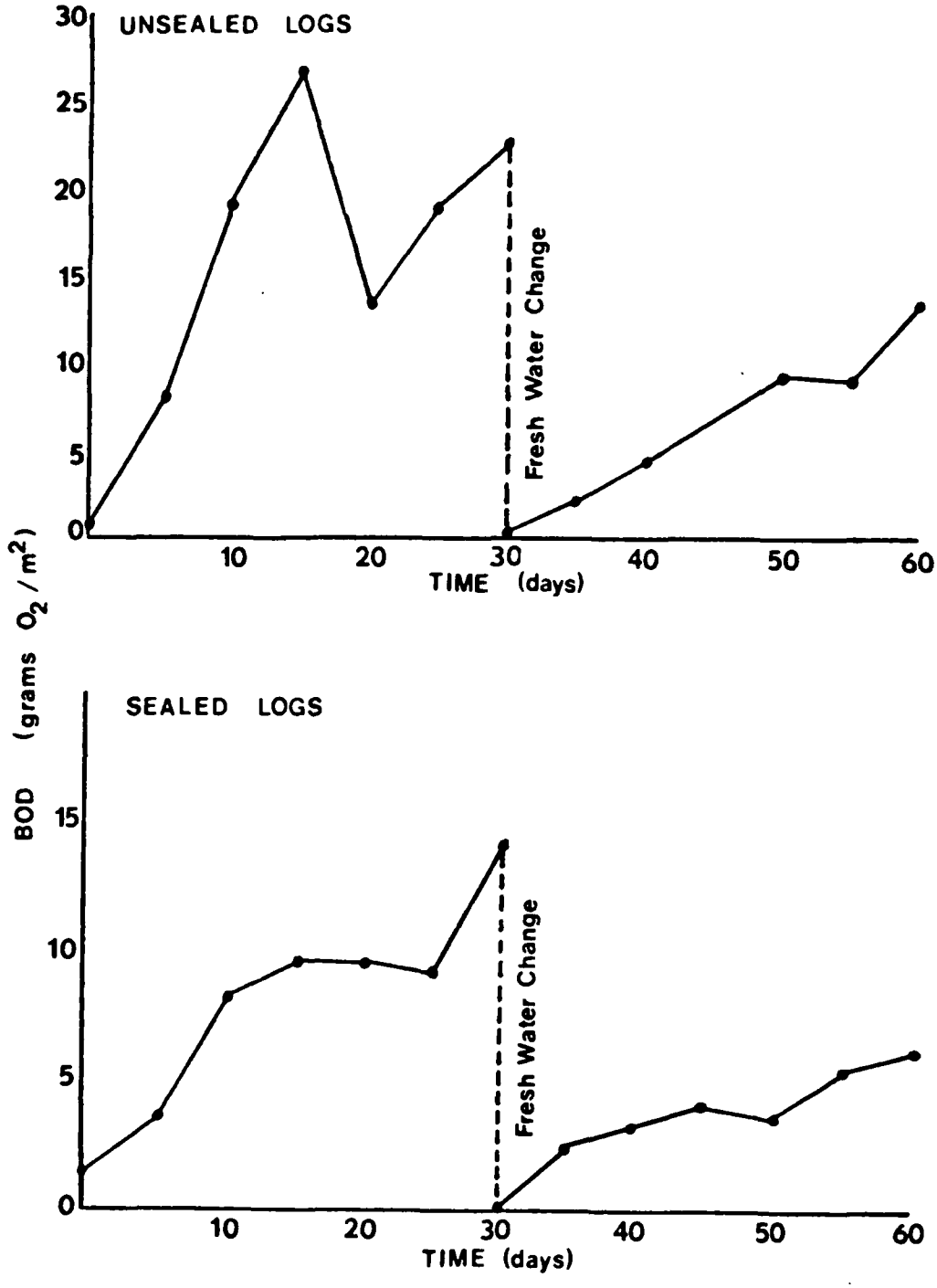

Figure 10. Biochemical oxygen demand (BOD_5) values (expressed as grams O_2/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

COD values for unsealed logs were considerably higher than those for logs with sealed ends (Figure 11). A high of 200 g/m^2 COD was measured on the 30th day of leaching in unsealed logs as opposed to approximately 27 g/m^2 for sealed logs in the same period. This trend was maintained for the second leaching in fresh water for both sets of logs where 109 g/m^2 COD was reached for unsealed logs and only 17 g/m^2 COD by sealed logs.

The rate of leaching for unsealed logs averaged approximately 6.6 g/m^2 per day in the first 30 days and 3.6 g/m^2 per day in the second period. Sealed logs produced only 0.9 g/m^2 and 0.7 g/m^2 per day respectively for the two consecutive leaching periods. Dissimilarity between the two leaching rates for the two sets of logs, again, points out the effect of sealing the crosscut ends.

BOD and COD values, when viewed together as a ratio (BOD_5:COD), can give a measure of the biodegradability of the substance under examination. The ratios for both sealed and unsealed logs ranged from 0.73 to 0.08 (Table 4). This compares with BOD_5:COD ratios for glucose and raw domestic sewage of 0.70 and 0.50 respectively (Schaumburg 1972). Higher ratios for sealed logs ranged from 0.73 to 0.28, indicating the leaching of highly biodegradable organic substances from the bark. This, however, is not believed to be a product of the bark, but highly soluble wood sugars leached from the cambium growth layer just beneath the bark. Wood sugars are found in smaller concentrations in heartwood than in sapwood, the active growth tissue (Schaumburg 1972). Servizi et al. (1971) had similar results when comparing outer bark to actively growing inner bark.

The highest BOD_5:COD ratio for unsealed logs was 0.35 which occurred on the 5th day of leaching. This indicates a rapid release of the highly

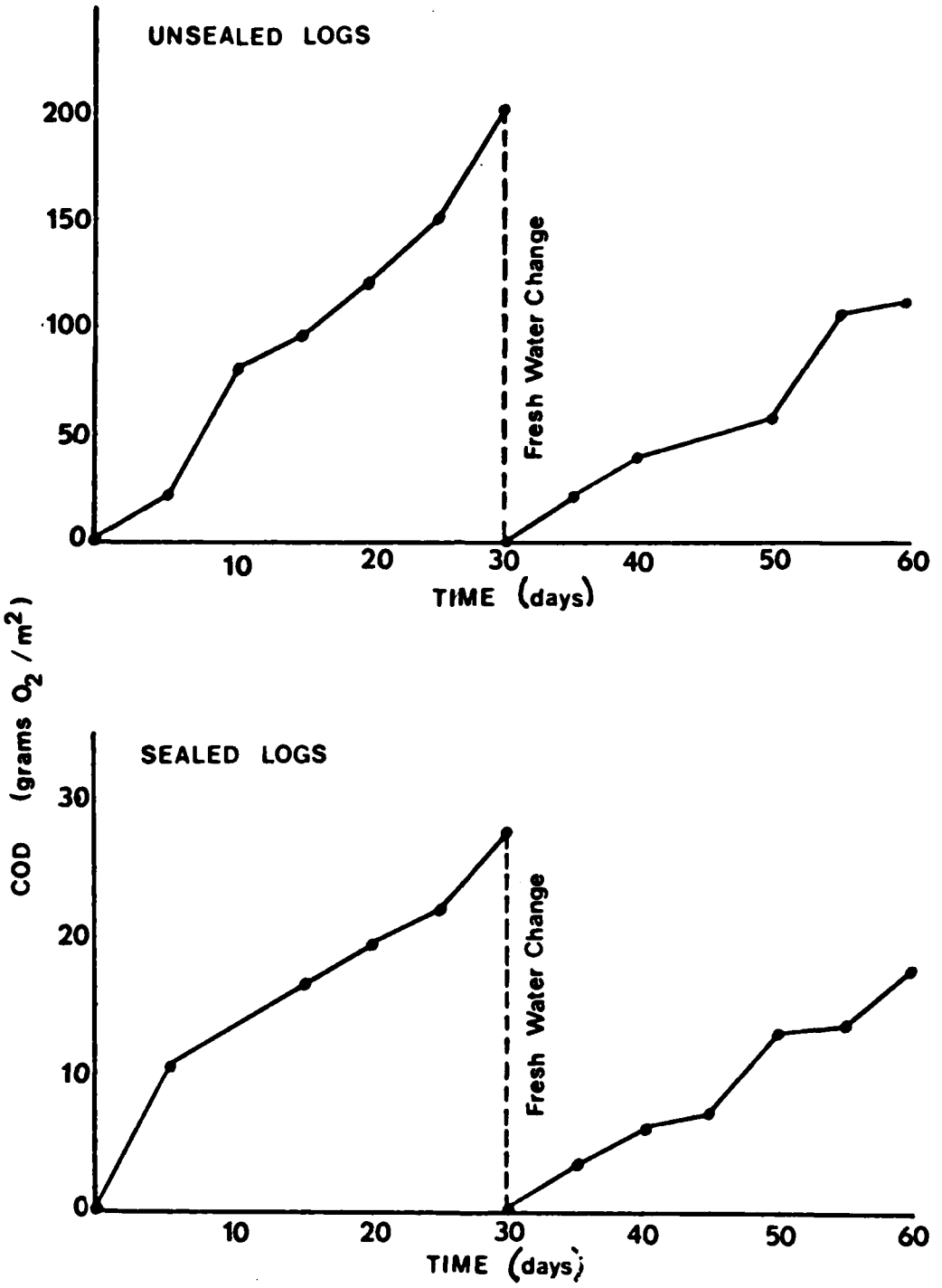

Figure 11. Chemical oxygen demand (COD) values (expressed as grams O_2/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

Table 4. Biochemical oxygen demand (BOD_5), COD, and BOD_5:COD values for water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

Days of Leaching	BOD_5 (g/m^2)	COD (g/m^2)	BOD_5:COD
Unsealed Logs			
5	7.8	22.0	0.35
10	19.3	82.1	0.24
15	26.6	95.0	0.28
20	13.4	117.7	0.11
25	19.1	152.1	0.13
30	22.2	200.5	0.11
(Fresh water change)			
35	2.1	19.6	0.11
40	4.3	38.9	0.11
50	9.4	57.5	0.16
55	8.9	105.1	0.08
60	13.2	109.2	0.12
Sealed Logs			
5	3.5	10.6	0.33
10	8.2	--	--
15	9.3	16.6	0.56
20	9.2	18.2	0.49
25	8.8	21.9	0.40
30	13.9	27.2	0.51
(Fresh water change)			
35	2.4	3.3	0.73
40	2.9	5.3	0.55
45	3.9	6.6	0.59
50	3.7	13.3	0.28
55	5.3	13.9	0.38
60	5.9	16.6	0.36

soluble sugars as well as the more complex organic substances into the holding waters. The much lower ratios during the remaining 25 days of leaching indicate lower percentages of these more readily degradable substances.

Schaumburg (1972) found BOD to be as high as 14 g/m^2 and COD to average 65 g/m^2 for Douglas fir and ponderosa pine logs in a 40 day leaching period. This did not compare closely to a high BOD of approximately 27 g/m^2 and COD high of 200 g/m^2 found in this experiment. The apparent difference is best explained by the younger aged trees used in this experiment. Trees used in this experiment averaged approximately 38 years old, while 68 years was the average age of trees used by Schaumburg. Younger trees, which have a higher percentage of sapwood to heartwood, produce 2 to 3 times more soluble organics per submerged surface area than do older trees (Schaumburg 1972). This and the fact that one species used in these experiments, western redcedar, has the highest percentage of water soluble extractives of any major coniferous species (Barton and MacDonald 1971).

Phosphate

There are few references in the literature regarding nitrate and phosphate contribution of wood and bark to holding waters. Schaumburg (1972) reported that neither of these substances appears in significant quantities in coniferous woods to be leached. Hoffbuhr et al. (1971), in a study of log holding ponds, found nitrates and phosphates to be released in amounts great enough to support increased biological growth. An average of 0.76 mg/l phosphate and 0.68 mg/l nitrates were reported in these ponds. Hoffbuhr found that the concentrations of both nitrates and phosphates increased with the increase of BOD and COD. This fact strongly suggests some addition from floating logs. Both studies, however, reported bottom deposits and the water supply to be the most important sources of the two nutrients.

Results of this study show high levels of nitrates and phosphates for both sealed and unsealed logs. Unsealed logs generated greater quantities of each substance. Phosphate concentrations for the unsealed logs reached 0.20 g/m^2 in the first 5 days of leaching and continued to increase to a high of 0.55 g/m^2 on the 30th day of the experiment (Figure 12). This is an average daily rate of 0.019 g/m^2 per day, with the highest rate 0.036 g/m^2 per day occurring in the first 5 days of leaching. The second 30 days of leaching produced an additional 0.28 g/m^2 at an average rate of 0.009 g/m^2 per day.

Sealing the crosscut ends reduced leaching of phosphate (Figure 12). In the first 30 days of leaching only 0.12 g/m^2 were produced. These concentrations did not appear until after 15 days of leaching. A slightly greater amount of phosphate was produced in the second 30 day period when a total of 0.20 g/m^2 was leached. The average rate of increase was approximately 0.005 g/m^2 per day for both runs.

The delay of 15 days before the appearance of phosphates sheds doubt on the contribution of bark in the leaching of this substance. It might indicate slowed radial leaching through the bark from the woody tissues below. This point is emphasized by the fact that in the second 30 day period leaching of phosphate occurred in the first 5 days, when the pores leading through the bark to the wood tissues had presumably been opened.

Nitrate

Nitrate values, although not as high as phosphate, were a significant nutrient input. Unsealed logs produced 0.10 g/m^2 nitrates in the first 30 day leaching period and 0.06 g/m^2 was attained in the second 30 days (Figure 13). This represents an average daily leaching rate of 0.003 g/m^2 and 0.002

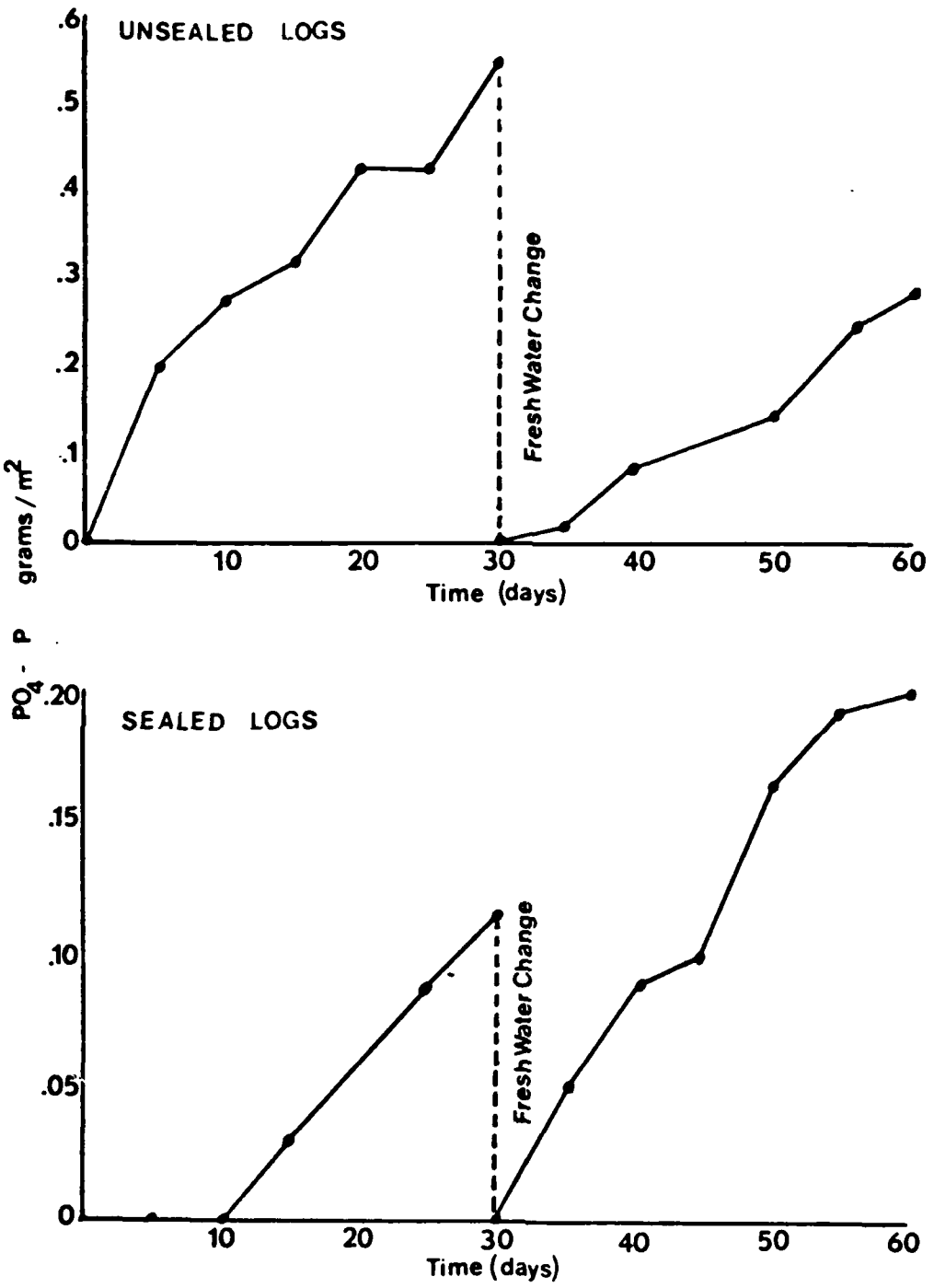

Figure 12. Phosphates (expressed as g/m^2 of submerged log surface area) in water containing sealed and unsealed logs, floating half submerged for two consecutive thirty day periods, 1974-1975.

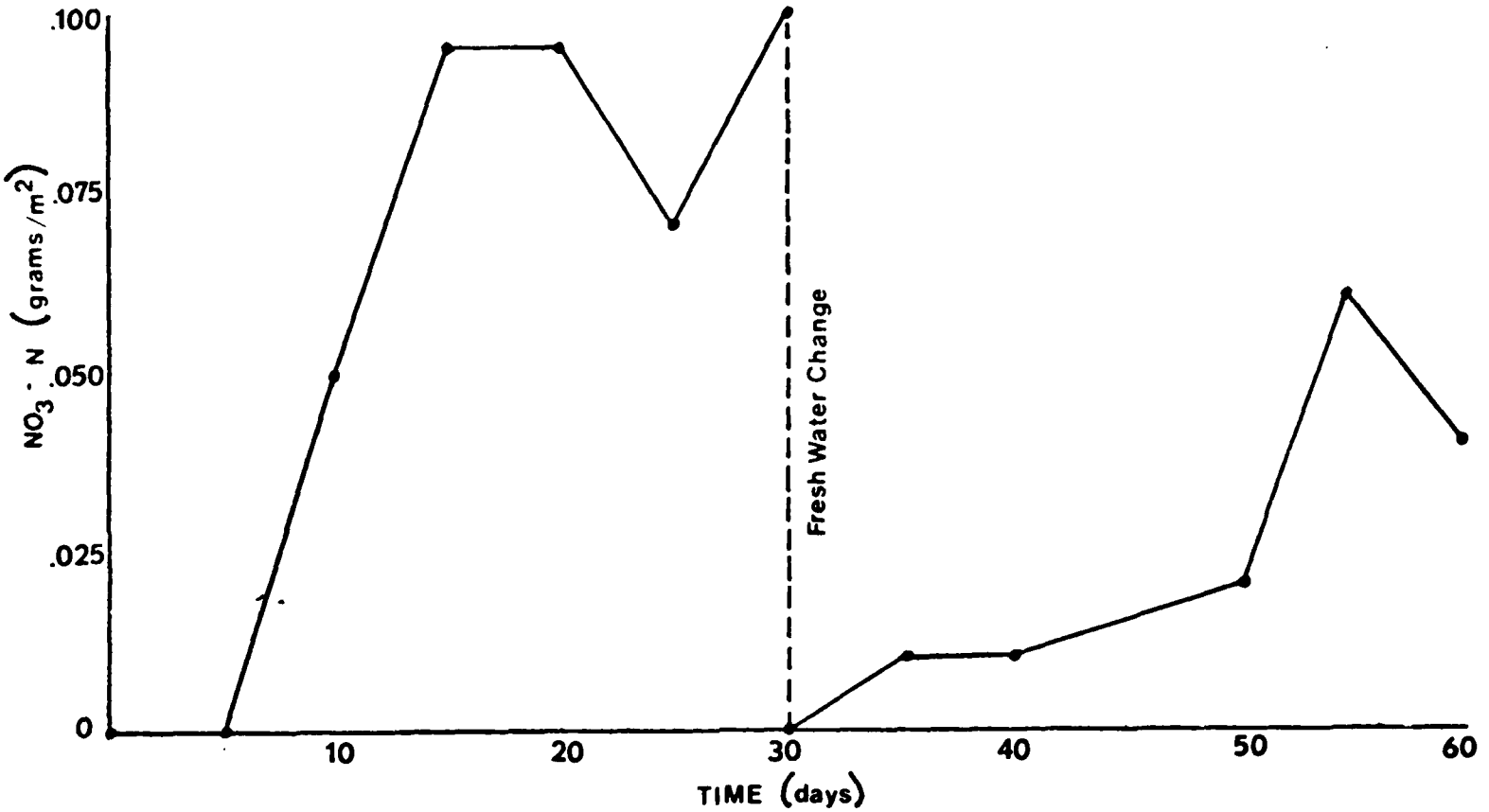

Figure 13. Nitrate-nitrogen (expressed as g/m^2 of submerged log surface area) in water containing unsealed logs, floating half submerged for two consecutive thirty day periods, 1974.

g/m^2 respectively. The greatest rate occurred between the 5th and 15th day of the initial leaching when an average of 0.009 g/m^2 per day was released.

Bacterial utilization of nitrates occurred in both the first and second periods (Figure 13). For unsealed logs in both periods a decline in nitrate concentrations near the ends of the periods suggests that nitrate leaching is nearing completion, or at least to a point where utilization is in equilibrium with leaching.

The leaching rate of nitrates from the sealed logs appeared not to be great enough to overcome utilization of this substance by the bacterial community present. In both 30 day periods nitrates in the test tank decreased below the level of that in the control.

Field Application

It is the purpose of this section to relate the preceding experimental findings to the actual reservoir situation. By using a formula set forth by Schaumburg (1972) and data from the species used in this study, it is possible to convert the chemical results obtained from a 30 cm log section into the amounts leached from a full sized log floating in the reservoir. The following formula was first developed by Graham and Schaumburg (1969) and later modified by Schaumburg (1972). It was developed for extrapolation from laboratory test logs to the full sized logs in the field. This formula was further modified to exclude the correction for the percent of missing bark for each log because laboratory data collected did not take this into consideration.

$$T = \left[(D)\ (A_c)\right] + \left[(f_1)\ (B\text{-}D)\ (A_e)\right]$$

T = Total leachates contributed from full sized logs (grams)

$$B = \frac{\text{grams leached from test logs (ends unsealed)}}{\text{cylindrical area submerged } (m^2)} \quad \begin{matrix}\text{(Table 2)} \\ \text{(Table 1)}\end{matrix}$$

$$D = \frac{\text{grams leached from test logs (ends sealed)}}{\text{cylindrical area submerged } (m^2)} \quad \begin{matrix}\text{(Table 3)} \\ \text{(Table 1)}\end{matrix}$$

A_e = Total submerged end area of field log (m^2) = .64/1000 bd ft

A_c = Total submerged cylindrical area of field logs (m^2) =

18.87/1000 bd ft

$$f_1 = \frac{\text{cylindrical area of test logs}}{\text{end area of test logs}} \quad \begin{matrix}\text{(Table 1)} \\ \text{(Table 1)}\end{matrix}$$

Values for A_e and A_c are an average for ponderosa pine and Douglas fir logs measured in the field by Schaumburg (1972). Table 5 contains the calculated quantities of leachates produced by a hypothetical log raft. Experimental results used were from day 30 for the unsealed logs (Table 2).

When these results were projected over the entire reservoir and to a 10 meter epilimnion, they would be diluted by a factor of 4.0×10^{13} and 7.0×10^{11} respectively. If the entire 185 MBF of saw and pole timber that existed in the reservoir basin prior to the filling were leached at one time, the resulting COD would only be an addition of 5190 kg/day or .0000012 mg/1/day to the entire reservoir.

Problems could arise if log rafts were to occur in small bays isolated from significant wind activity. A small bay of 200,000 square meters with a mean depth of 15 meters would contain approximately 3.0×10^9 liters of water. This bay would contain approximately 2.0×10^9 liters in a 10 meter epilimnial layer. A 181 kg COD per day addition would result in an addition of approximately 0.1 mg/1 COD/day and .03 mg/1 BOD/day to the epilimnion.

Nutrient addition from this log raft would not be high; after one month, .001 mg/1 PO_4-P would be leached.

Table 5. Addition rates of leachates produced by a hypothetical log raft of 100,000 m^2, all bark intact, floating half submerged for 1 day and 1 month.

	One Day					One Month				
	Total Constituents Leached	Addition rate per day if diluted in: Entire Reservoir	Entire Epilimnion 10 m thick	200,000 m^2 Bay	200,000 m^2 Bay - 10 m Epilimnion	Total Constituents Leached	Addition rate per day if diluted in: Entire Reservoir	Entire Epilimnion 10 m thick	200,000 m^2 Bay	200,000 m^2 Bay - 10 m Epilimnion
	mg per liter					mg per liter				
Color (units)	7.7×10^{4}	1.9×10^{-9}	1.1×10^{-7}	2.6×10^{-5}	3.9×10^{-5}	2.3×10^{6}	6.0×10^{-8}	3.0×10^{-6}	8.0×10^{-4}	1.2×10^{-3}
M.O. Alk. (mg)	2.0×10^{8}	5.0×10^{-5}	3.0×10^{-3}	7.0×10^{-2}	1.0×10^{-1}	5.9×10^{9}	1.5×10^{-3}	9.0×10^{-2}	2.0	2.4
CO_2 (mg)	1.5×10^{8}	4.0×10^{-5}	2.0×10^{-3}	5.0×10^{-2}	8.0×10^{-2}	4.6×10^{9}	1.2×10^{-3}	8.0×10^{-2}	1.5	2.3
Tannin (mg)	6.7×10^{7}	1.7×10^{-6}	9.0×10^{-5}	2.2×10^{-2}	3.4×10^{-2}	2.0×10^{9}	5.0×10^{-5}	3.0×10^{-3}	7.0×10^{-1}	1.0
BOD_5 (mg)	5.4×10^{7}	1.4×10^{-6}	8.0×10^{-5}	1.8×10^{-2}	2.7×10^{-2}	1.6×10^{9}	4.0×10^{-5}	2.0×10^{-3}	5.0×10^{-1}	8.0×10^{-1}
COD (mg)	1.8×10^{8}	5.0×10^{6}	3.0×10^{-4}	6.0×10^{-2}	9.0×10^{-2}	5.4×10^{9}	1.4×10^{-4}	8.0×10^{-3}	1.8	2.7
PO_4-P (mg)	1.0×10^{6}	3.0×10^{-9}	1.0×10^{7}	4.0×10^{-5}	5.0×10^{-4}	3.0×10^{6}	8.0×10^{-8}	4.0×10^{-5}	1.0×10^{-3}	1.5×10^{-3}
NO_3-N (mg)	7.0×10^{5}	2.0×10^{-9}	1.0×10^{-6}	1.0×10^{4}	4.0×10^{-4}	2.1×10^{6}	5.0×10^{-8}	3.0×10^{-5}	0.7×10^{-3}	1.0×10^{-3}

In-situ Bioassay

A total of 6 in-situ bioassays were conducted in the summer and fall of 1974. Three of these bioassays have been selected for detailed discussion because they best illustrate the response to log leachates of the four most prominent summer and fall algal genera in Dworshak Reservoir. The three remaining bioassays will be discussed in more general terms.

Leachates used in each bioassay contained a total of 0.62 mg/l orthophosphate, 0.11 mg/l nitrate-nitrogen and 225.8 mg/l total carbon. Table 6 indicates the amounts of these nutrients contributed to the polyethylene bags after inoculation and the initial nutrient concentration prior to each bioassay.

A considerable amount of work has been done regarding nutrient enrichment and primary production. Powers, Schults, Malueg, Brice and Schuldt (1972), in in-situ bioassays of Minnesota and Oregon lakes, found that phosphorus was the primary nutrient controlling algal growth. Similar results were obtained by Maloney, Miller and Shiroyama (1972) in laboratory assays using Selenastrum capricornutum as a test species. In both studies, nitrogen produced some growth stimulation while carbon proved to have little or no effect on increased production.

The first three bioassays were conducted between May 7th and June 20th, 1974. Log leachate concentrations added to 40 liters of reservoir water were: 0%, .25%, .50%, 1.00%, 1.50%, 2.00%, and 2.50% of the bag volume. Dominant algae in these bioassays were diatoms with Melosira being the most numerous genus throughout all three bioassays. Because no other algal genus was present in large numbers, these three bioassays have been combined to show the response to leachate concentrations. Production, as measured by

Table 6. Initial nutrient levels of Dworshak Reservoir water prior to each bioassay (1-6), conducted May-October, 1974; and nutrient levels contributed by the addition of log leachates to 40 liters of Dworshak Reservoir water in polyethylene bags, 1974.

	NO_3-N (mg/1)	PO_4-P (mg/1)	Total Carbon (mg/1)
Bioassay			
No. 1	.0300	.0050	9.10
No. 2	.0230	.0050	6.20
No. 3	.0210	.0250	6.10
No. 4	.0220	.0050	4.00
No. 5	.0160	.0050	4.00
No. 6	.0400	.0140	14.50
Leachate (%)			
0.125	.0001	.0008	.28
0.25	.0003	.0016	.56
0.50	.0006	.0031	1.13
1.00	.0011	.0062	2.26
1.25	.0014	.0078	2.82
1.50	.0017	.0093	3.39
2.00	.0022	.0124	4.52
2.50	.0028	.0155	5.65

chlorophyll a concentrations, on the last day of the experiment was greater than the control in all cases (Figure 14). Differences between sample means were highly significant for all three bioassays (T = 98.13**, T = 51.84**, and T = 93.92**).

Bioassay No. 4 was conducted July 1-5, 1974. Log leachate concentrations added to 40 liters reservoir water were: .0%, .125%, .50%, and 2.5%. At the beginning of the experiment, dominant algal genera were Anabaena (blue-green), Melosira (diatom), and Mougeotia (green). The numerical ratio of dominance was approximately 1.5:1.3:1.0 respectively. Total algal numbers were approximately 115,000 cells/1.

Following 24 hours of incubation, Melosira became the dominant algal genera while Anabaena and Mougeotia declined to very low numbers (Figure 15). The ratio of dominance at this point was 8:3:1 for Melosira, Anabaena, and Mougeotia sp. respectively. Chlorophyll a concentrations during this same 24 hour period increased from an initial 27 mg/m^3 to an average 43 mg/m^3 in all treatments (leachate concentrations). Melosira remained the dominant genus throughout the entire run, averaging approximately 120,000 cells/1, while the treatment average for Anabaena and Mougeotia was less than 25,000 cells/1 for the same period. The control bag during this bioassay remained below 60,000 cells/1 for total cell counts.

Examination of the treatment response for total cell counts of each algal genera and for chlorophyll a best illustrates this shift in dominance (Figure 16). After 5 days total diatom numbers increased with the increase of log leachate treatments (R^2 = .90**), while green algae responded negatively to treatments (R^2 = -.77**). Essentially no growth occurred at the 2.5% concentration, indicating inhibition or toxicity.

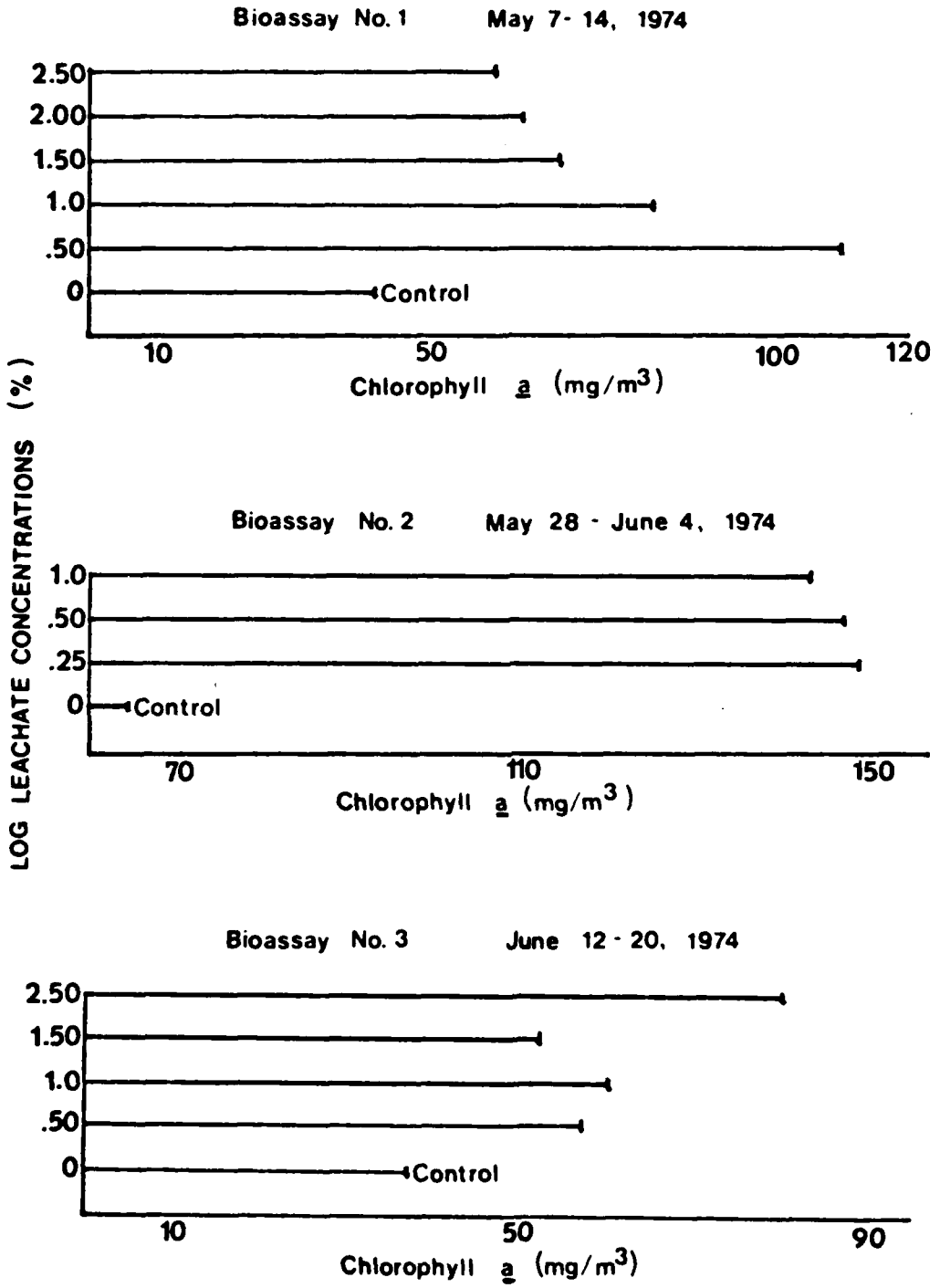

Figure 14. Chlorophyll a in 8 day bioassays at various concentrations of log leachates in Dworshak Reservoir water, bioassays Nos. 1-3, conducted May 7-June 20, 1974.

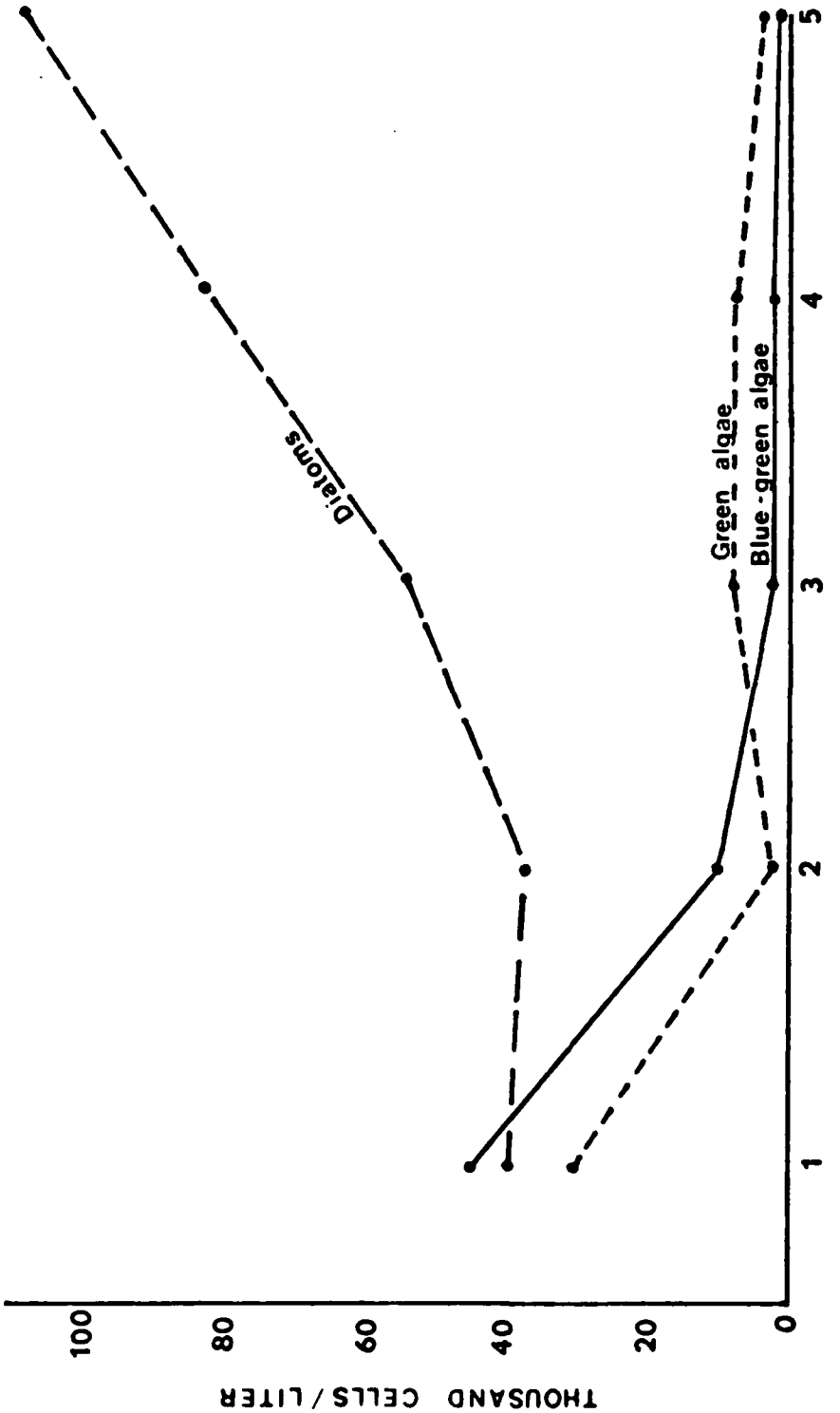

Figure 15. Algal response (average of treatments) to log leachates in 40 liters of Dworshak Reservoir water. Bioassay No. 4 conducted July 1-5, 1974.

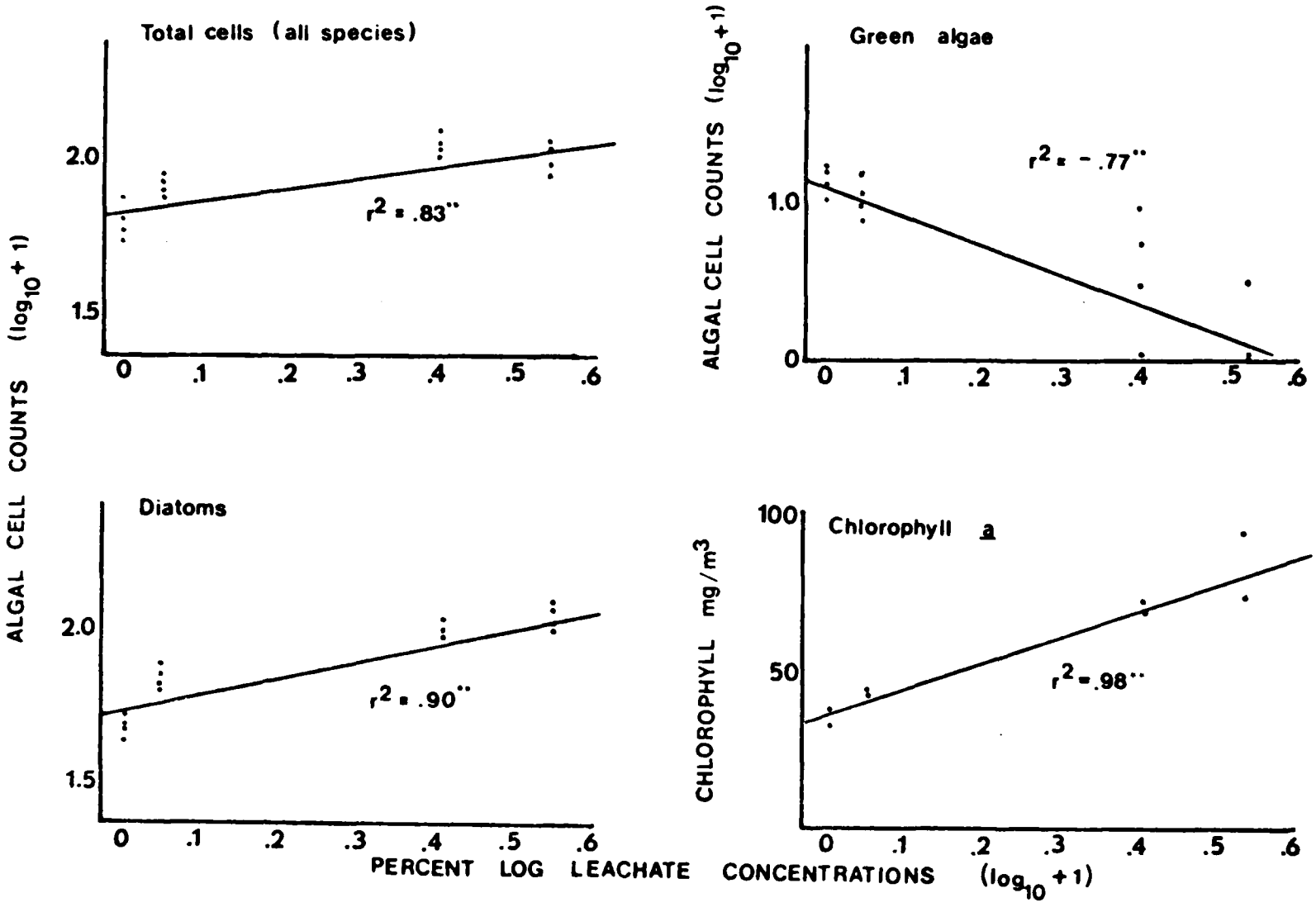

Figure 16. Algal cell counts and chlorophyll a on the 5th day of bioassay No. 4, conducted on Dworshak Reservoir, July 1-5, 1974.

To supplement actual cell counts, chlorophyll a measurements were taken daily during each run. Fifth day chlorophyll a measurements showed an increase with the increase in percent log leachate (R^2 = .98**) (Figure 16). Anabaena responded negatively to the bag environment rather than the leachate inoculant. Anabaena numbers in both the control and treatment bags decreased while lake numbers remained high. The response for all genera was positive (R^2 = .83**).

Bioassay No. 5 was conducted August 23-27, 1974. Leachate concentrations added to 40 liters of reservoir water were: 0%, .125%, .50%, 1.50%, and 2.50%. Algal dominance at the start of the experiment, in descending order, was green algae (Chlorella and Ankistrodesmus); the dinoflagellate, Dinobryon; blue-green algae, Anabaena; and diatoms, Diatoma and Cyclotella. Total algal cells at the start of the run were approximately 660,000 cells/l with a ratio of 123:10:4:1 (greens:dinoflagellates:blue-greens:diatoms). In addition, unknown rod shaped bacteria (100,000 cells/l) were present in the reservoir at the beginning of the experiment.

Average numbers of diatoms and dinoflagellates remained relatively stable throughout the experiment (Figure 17). Blue-green algae declined to 0 cells/l for the last 48 hours of the experiment. Green algae dropped sharply in numbers from approximately 500,000 cells/l to approximately 110,000 cells/l during the first 24 hours of the experiment. Average numbers of bacteria increased slowly in the first 48 hours then increased to over 1,500,000 cells/l after 5 days (Figure 17). Green algae, even though remaining in low numbers, did show a positive response to treatments after 5 days (R^2 = .83**) (Figure 18). All treatments resulted in dinoflagellates declining to numbers below those of the controls (R^2 = -.34*), even though

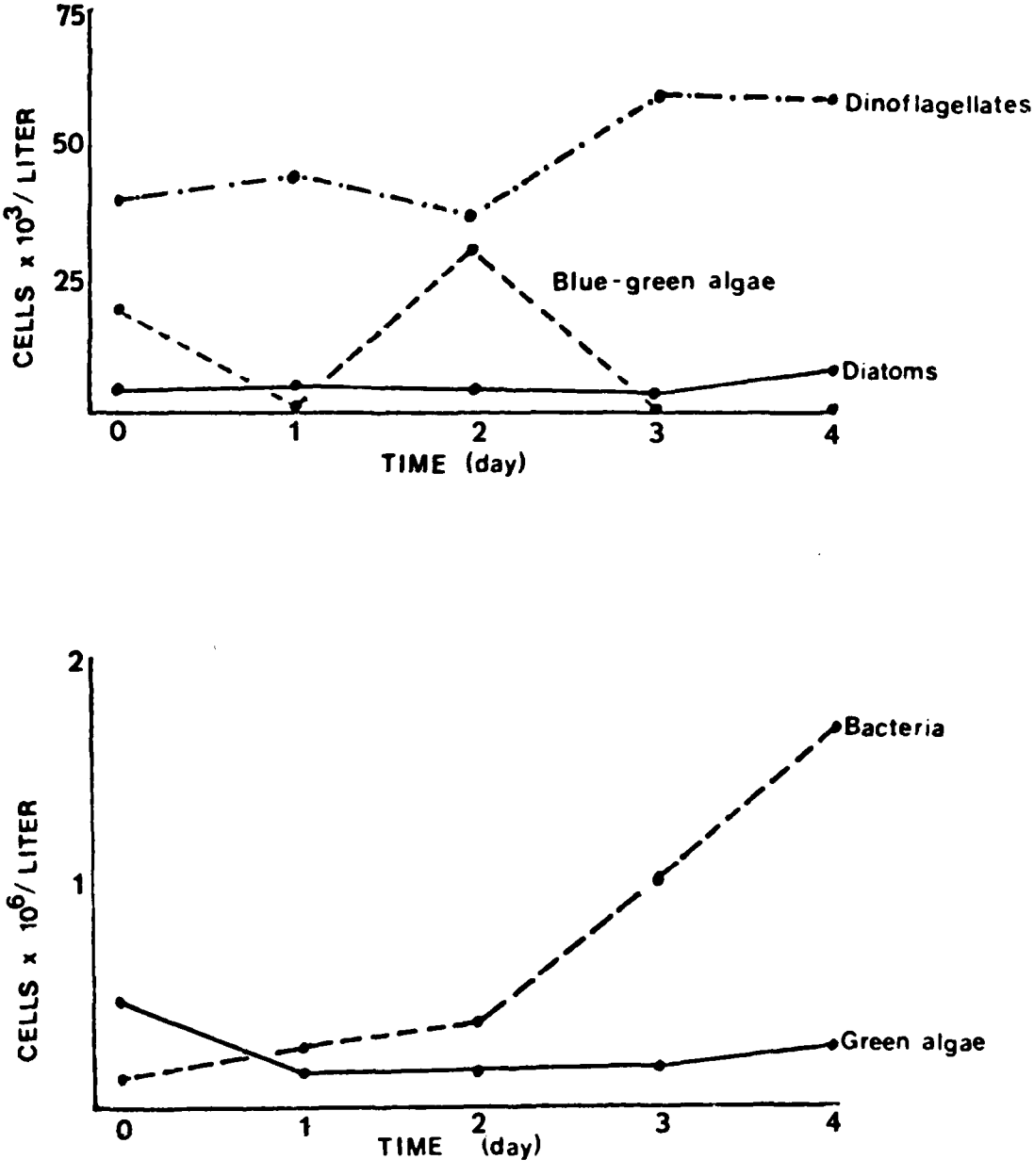

Figure 17. Algal response (average of treatments) to log leachate in 40 liters of Dworshak Reservoir water. Bioassay No. 5 conducted August 23-27, 1974.

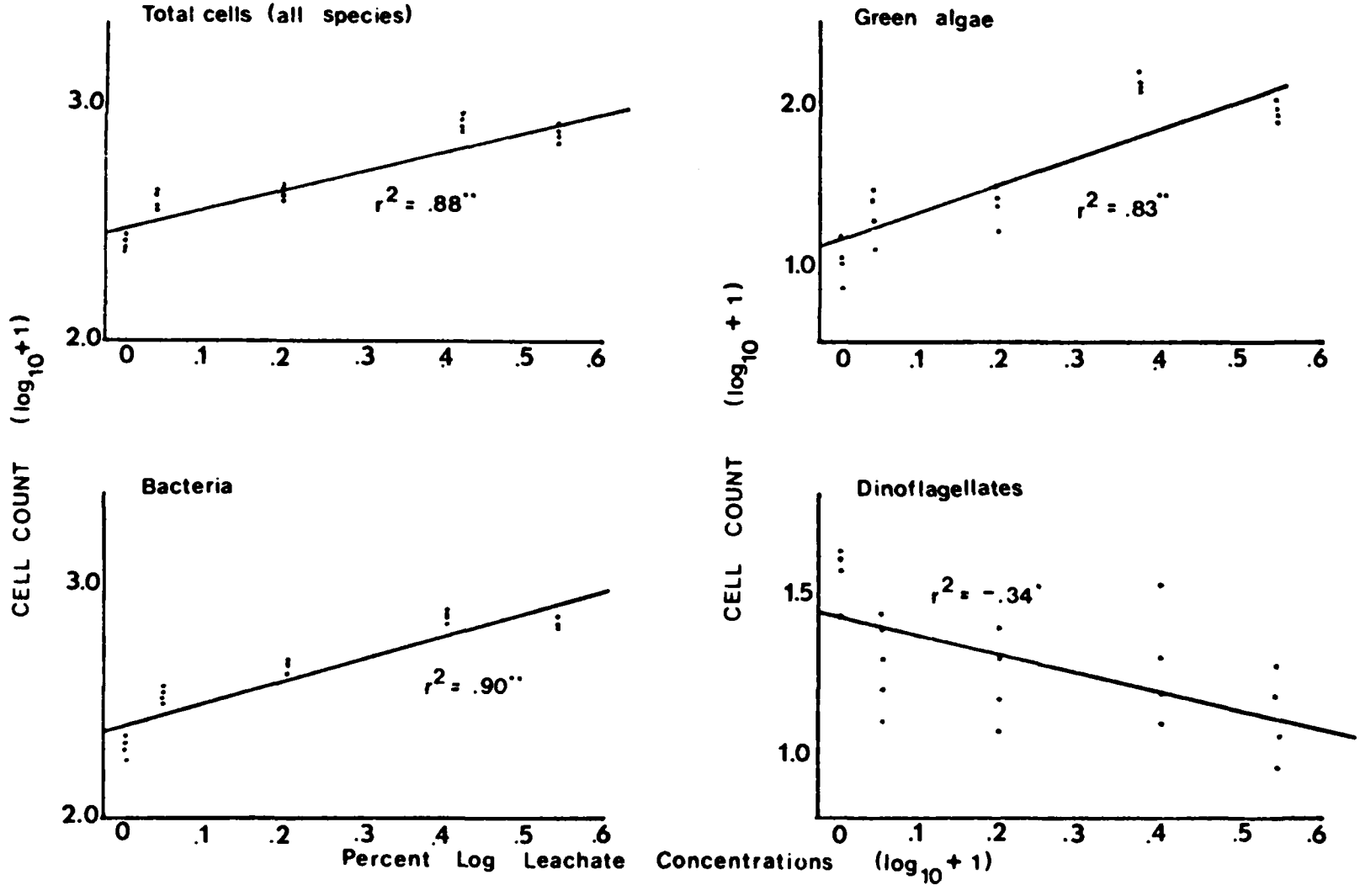

Figure 18. Algal and bacterial cell counts on the 5th day of bioassay No. 5 conducted on Dworshak Reservoir, August 23-27, 1974.

Dinobryon reached bloom proportions (1,200,000 cells/l) in the reservoir during the experiment. A bag effect is thus indicated as well as inhibition by the leachate. The toxic response of Dinobryon is best explained by the inhibition of this genus by the presence of PO_4-P. Concentrations ranging from 1.0 to 5.0 mg/m^3 have been shown to inhibit species of this genus (Hutchinson 1967). Measured PO_4-P concentrations for log leachates in all bioassays ranged from 0.8 to 15.5 mg/m^3. Bacterial response followed a pattern similar to that of the diatoms in the previous run, showing a positive response to the leachate treatments (R^2 = .90**). Diatom numbers remained low throughout the experiment. Chlorophyll a concentrations showed a positive response to treatments but were not significant at the levels tested (R^2 = .49NS).

Bioassay No. 6 was conducted October 14-18, 1974. To establish the validity of polyethylene bags as an experimental apparatus, two sets of treatment and control bags were run simultaneously. The leachate concentrations added to 40 liters of reservoir water were: 0.25%, 1.25%, and 2.50%.

During the duration of this experiment one control bag and a 0.25% leachate bag were discarded because of leaks. For this reason, a meaningful statistical analysis between all treatment bags is not possible. All treatments (in duplicate sets), represented by total cells, were below the controls on the 1st day of the bioassay. This, as in the previous run, indicates an initial toxic response (Figure 19).

Algae genera for this bioassay, in order of dominance at the start of the run, were: Anabaena, Aphanizomenon, Gleocystis, Tetraspora, Melosira, and Dinobryon. The ratio of dominance was approximately 6:3:2:1 respectively for blue-greens, greens, diatoms, and dinoflagellates. This order of dominance

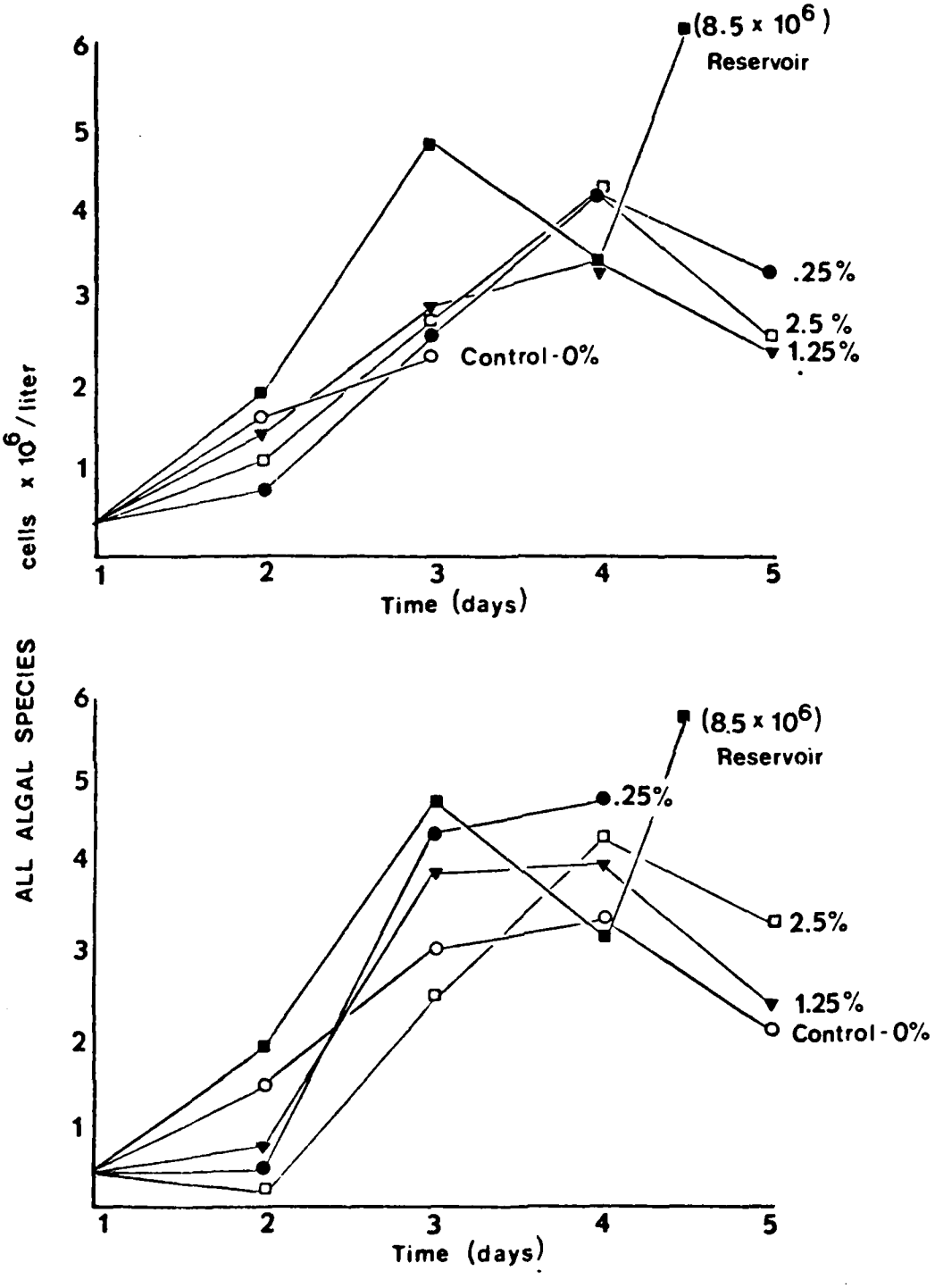

Figure 19. Algal response to treatments for duplicate bioassays conducted at Dworshak Reservoir. Bioassay No. 6, October 14-18, 1974.

remained stable throughout the experiment. Total algal cells at the start of the bioassay was approximately 365,000 cells/l.

An analysis of treatment response for the 5th day shows no significant changes for all genera except Dinobryon which registered a negative response (R^2 = -.73**) to treatments (Figure 20). Again, this negative reaction to treatments is believed to be due to the inhibition of this genus by the presence of PO_4-P. Chlorophyll a trends were not significant.

The lack of response for most genera in this bioassay might be explained by the fact that the experiment was initiated during a rapid algal growth period. Reservoir numbers reached bloom proportions (8,500,000 cells/l) on the last day of the run. This indicates that conditions for growth in the reservoir were optimum and the addition of log leachates had little effect as a biostimulant. It may also be noted that blue-green algae, which has already demonstrated a negative response to the bag environment, was the dominant genus in the reservoir. Bag suppression might be slower to appear during the log growth phase, as indicated by the drop in numbers in both treatment and control bags on the last day of the bioassay (Figure 19).

In general, log leachates had a positive influence on natural algal production of the reservoir, measured by cell counts and chlorophyll a (Figure 21). It is apparent that the environment created by the polyethylene bags tends to increase algal numbers over those in the reservoir. This slight increase in production in the control bag (0% leachate) over the natural reservoir situation suggests the tendency of the bag environment toward eutrophy. An initial decline in algal numbers in the treatment bags to levels below both control and reservoir populations was noted in the first 24 hours. This lag in numbers is a reflection of a toxic response of certain algal

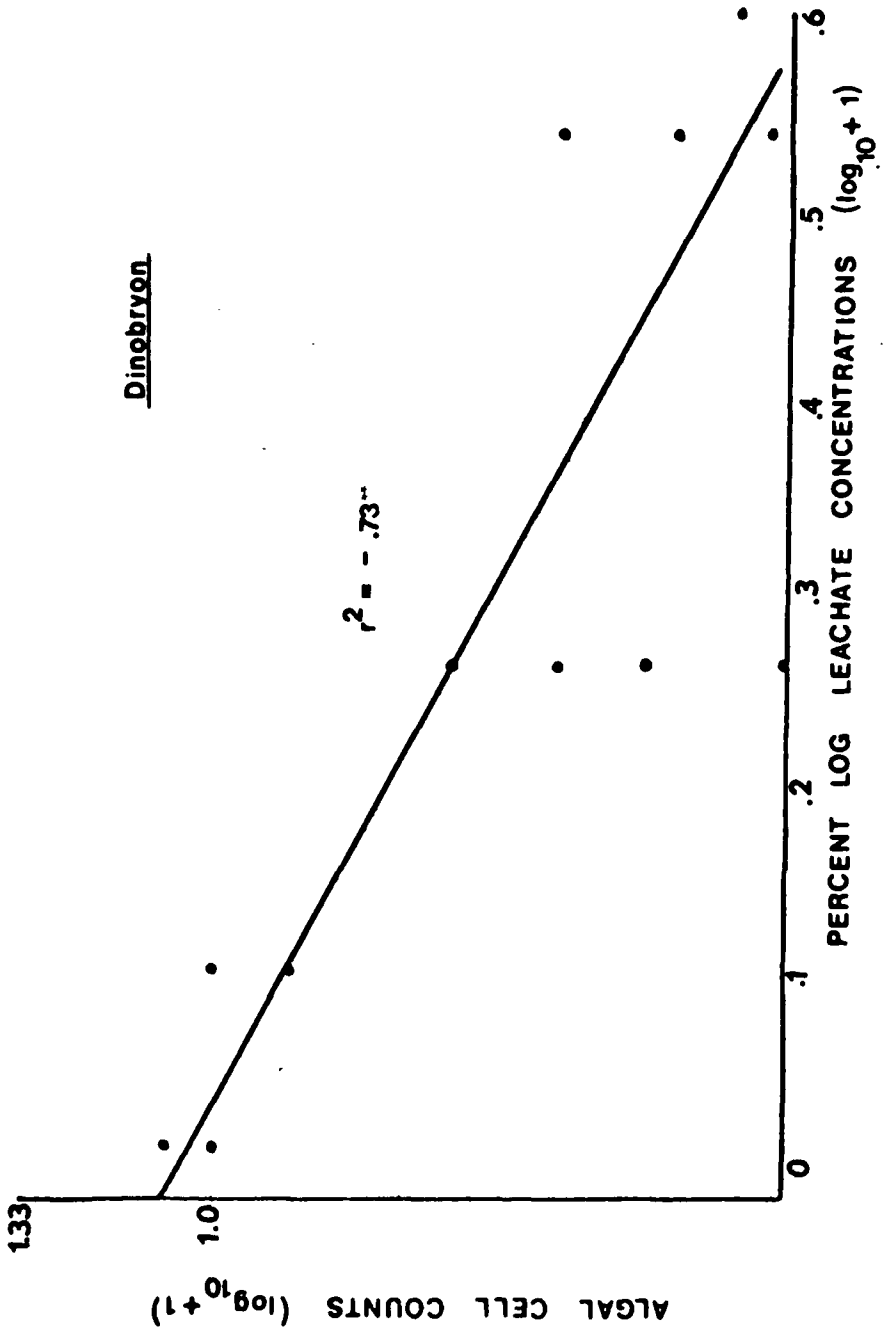

Figure 20. Treatment response (duplicates combined) for Dinobryon on the 5th day of bioassay No. 6 conducted at Dworshak Reservoir, October 14-18, 1974.

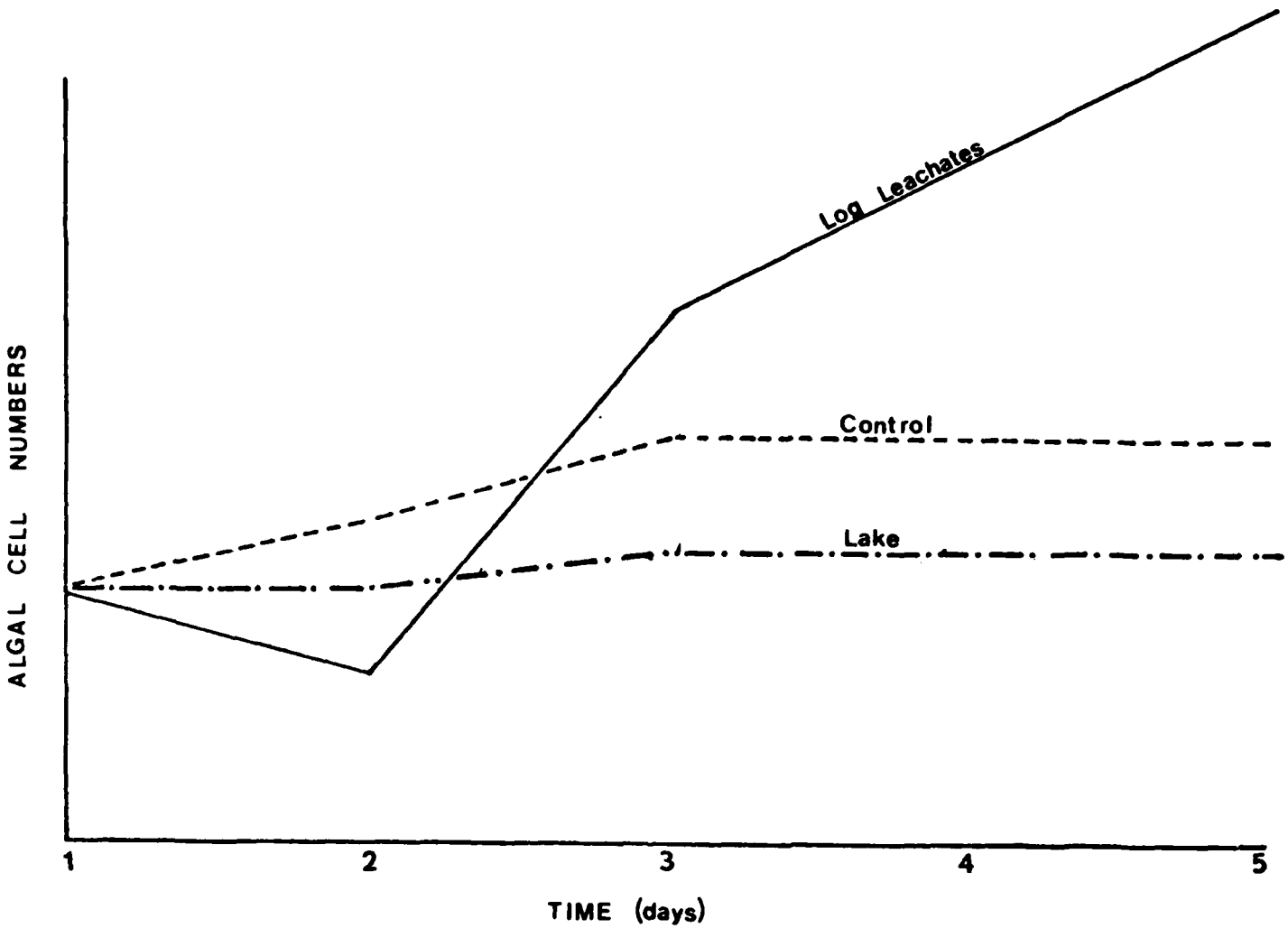

Figure 21. Generalized comparison of algal response to log leachates, control, and the reservoir environment over a 5 day period. Dworshak Reservoir, 1974.

genera to log leachates. An increase in chlorophyll a production coupled with a rise in algal numbers from day 2 through day 5 is caused by increased production by the species which dominates the bag environment.

CONCLUSIONS

1. Log leachates contributed organic substances which exert a BOD and COD on the holding waters. The amounts of these pollutants produced by floating logs was high (200 g/m^2 COD and 22.2 g/m^2 BOD), but are not believed to be a water quality problem due to the large dilution capacity of Dworshak Reservoir (4.0×10^{14} liters). Only in shallow protected bays, where logs are concentrated, will water quality degradation occur.
2. Woody tissues, rather than bark, were the source of most of the organic substances contributed by floating logs.
3. Coniferous logs, when placed in fresh water, reduced the pH of that water by 2.4 pH units per m^2 (wood and bark exposed) per m^3 of water. The leaching of woody tissues decreased the pH approximately twice as much as the leaching of bark.
4. Color, measured as tannin-like substances, was produced mainly from the woody tissues of floating logs.
5. Nitrate and phosphate levels found in coniferous logs was higher than expected. These high concentrations (0.55 g/m^2 PO_4-P and 0.10 g/m^2 NO_3-N) are believed to significantly add to the productivity of the reservoir.
6. Log leachates, when added to Dworshak Reservoir water in 40 liter polyethylene bags, increased algal production (measured as chlorophyll *a*) as much as three times over that of the control.
7. Some algal genera showed a toxic response to log leachates. This toxicity was demonstrated by a decrease in algal numbers with an increase in log leachate treatments.

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EPILIMNIAL PHYTOPLANKTON LOSSES AND ZOOPLANKTON POPULATION DYNAMICS IN DWORSHAK RESERVOIR, 1973-1974

Part 3

of

EARLY LIMNOLOGY OF DWORSHAK RESERVOIR

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	3-iii
LIST OF TABLES	3-vi
LIST OF FIGURES	3-vii
ABSTRACT	3-ix
INTRODUCTION	3-1
DESCRIPTION OF THE RESERVOIR	3-5
METHODS	3-6
SAMPLE STATIONS	3-6
PHYTOPLANKTON	3-6
Sampling and Counting	3-6
Biomass Estimation	3-7
Primary Production	3-7
Chlorophyll	3-8
ZOOPLANKTON	3-8
Sampling and Counting	3-8
Grazing Rate Determination	3-8
BACTERIA	3-9
TEMPERATURE AND TURBIDITY	3-9
TOTAL PHYTOPLANKTON LOSS RATE CALCULATIONS	3-10
Net Production Rate (P)	3-11
Biomass Change Rate (C)	3-19
GRAZING RATE DETERMINATION	3-20
SINKING RATE DETERMINATION	3-24
RESULTS AND DISCUSSION	3-25
PHYTOPLANKTON LOSS THROUGH GRAZING	3-25
Grazing Coefficient	3-25
Grazing Losses	3-26
PHYTOPLANKTON LOSS THROUGH SINKING	3-34
Sinking Rate Determination	3-34
Sinking Losses	3-37
PHYTOPLANKTON RECYCLED WITHIN THE EPILIMNION	3-38
Bacterial Concentrations and Phytoplankton Recycling	3-40

Page

RESULTS AND DISCUSSION (continued)

PRIMARY PRODUCTION EFFICIENCY 3-43
EPILIMNIAL CARBON BUDGET. 3-45
ZOOPLANKTON POPULATION DYNAMICS 3-46
Grazer Production. 3-46
Transfer Efficiency. 3-48
Assimilation Efficiency. 3-49
Zooplankton Birth Rates. 3-49
Grazing Selectivity. 3-50

CONCLUSIONS. 3-55

LITERATURE CITED 3-57

LIST OF TABLES

Table — Page

1. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (main reservoir station), March-December, 1973. 3-12

2. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (main reservoir station), March-November, 1974. 3-13

3. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (main reservoir station), March-December, 1973. 3-14

4. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (Elk Creek Arm station), March-November, 1974. 3-15

5. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (main reservoir station), March-December, 1973. 3-16

6. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (main reservoir station), March-November, 1974. 3-17

7. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (Elk Creek Arm station), March-December, 1973 and 1974 3-18

8. Fragilaria cell counts in grazing enclosures with and without zooplankton during July 3-5, 1973 in Dworshak Reservoir . 3-21

9. Calculation of zooplankton grazing rates on Fragilaria at 20 m from six in situ measurements in Dworshak Reservoir, 1973. 3-23

10. Phytoplankton biomass at 30 m as a percentage of epilimnial phytoplankton biomass 3-39

11. Monthly and annual epilimnial phytoplankton carbon budgets for 1973 and 1974 in Dworshak Reservoir (main reservoir station). 3-41

Tables (continued) Page

12. Monthly and annual epilimnial phytoplankton carbon budgets for 1973 and 1974 in Dworshak Reservoir (Elk Creek Arm station). 3-42

13. Comparison of annual quantities of phytoplankton carbon recycled within the epilimnion with average annual epilimnial total bacteria concentrations in Dworshak Reservoir, 1973 and 1974. 3-43

14. Zooplankton biomass (mgC/m^3) averaged through a 1 m, 10 m, and an oblique tow in Dworshak Reservoir during March-November, 1974 (main reservoir station) 3-47

15. Calculation of Daphnia schodleri and Bosmina longirostris instantaneous birth rates (b) in Dworshak Reservoir (main reservoir station), 1974. 3-50

LIST OF FIGURES

Figure — Page

1. Relationship of spring and summer turbidity to monthly average percentage of phytoplankton loss to zooplankton grazing in Dworshak Reservoir (main reservoir station), 1973 and 1974. 3-28

2. Relationship of spring and summer turbidity to monthly average percentage of phytoplankton loss to zooplankton grazing in Dworshak Reservoir (Elk Creek Arm station), 1973 and 1974. 3-29

3. Epilimnial phytoplankton biomass, composition, and loss to grazing in Dworshak Reservoir (main reservoir station), 1973 and 1974 3-31

4. Epilimnial phytoplankton biomass, composition, and loss to grazing in Dworshak Reservoir (Elk Creek Arm station), 1973 and 1974 3-32

5. Average phytoplankton biomass in the epilimnion (surface, 3 m, 6 m) compared to biomass below the epilimnion (30 m) in Dworshak Reservoir (main reservoir station), 1973 and 1974. 3-35

6. Average phytoplankton biomass in the epilimnion (surface, 3 m, 6 m) compared to biomass below the epilimnion (30 m) in Dworshak Reservoir (Elk Creek Arm station), 1973 and 1974. 3-36

7. Primary production to total chlorophyll ratio compared to total phytoplankton loss as an indicator of production efficiency in Dworshak Reservoir (main reservoir station), 1974 3-44

8. Duration of embryonic development in Daphnia ambigua and Bosmina longirostris at different water temperatures (from Kwik, J.K. and J.C.H. Carter, 1975) 3-52

9. Epilimnial phytoplankton concentrations and composition related to Daphnia schodleri and Bosmina longirostris instantaneous birth rates (b) in Dworshak Reservoir (main reservoir station), 1974. 3-53

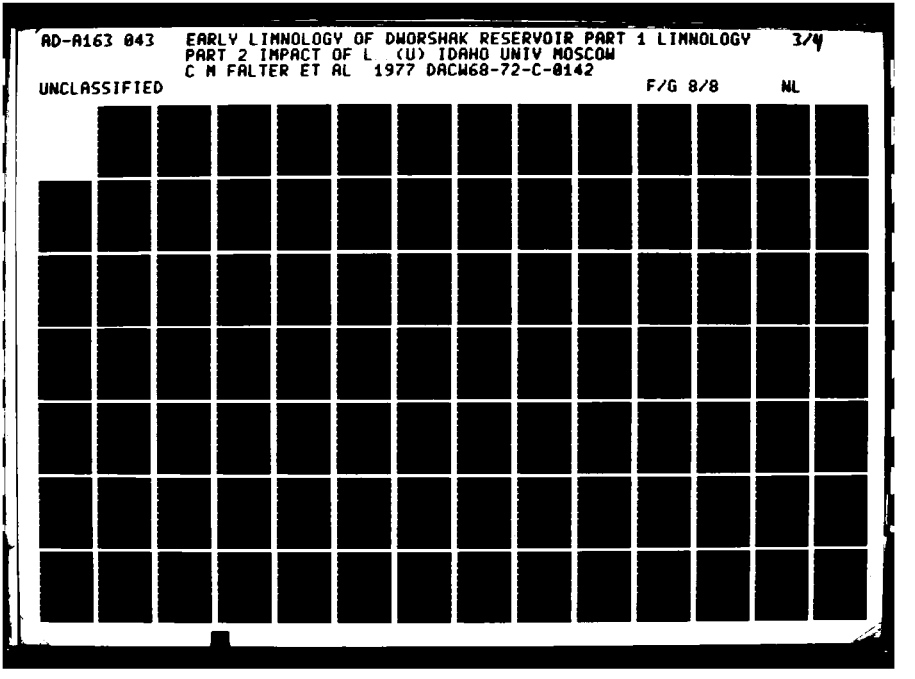
ABSTRACT

Primary production, phytoplankton biomass, and phytoplankton loss was monitored from March, 1973, through November, 1974 in the main body of Dworshak Reservoir and in Elk Creek Arm. Primary production averaged over both areas of reservoir during two years was 102.95 $mgC/m^3/day$; algal biomass averaged 18.91 mgC/m^3. Average annual biomass was about twice as concentrated in the main reservoir. In both areas of the reservoir production was higher in 1973 than in 1974 partially due to high turbidity during the spring of 1974.

Total phytoplankton loss from the epilimnion was calculated from biomass and production data. Total loss was partitioned into loss through grazing, loss through sinking, and recycling within the epilimnion. A grazing coefficient based on zooplankton filtering rate of Fragilaria was estimated from six in situ grazing experiments in 1973. The average grazing coefficient was 0.01429 m^3/mg zooplankton C/day. The loss of phytoplankton through grazing averaged 24.67 $mgC/m^3/day$. Grazing loss was reduced during seasons of high turbidity. Loss of phytoplankton from the epilimnion through grazing was 9.5% of the total loss.

Zooplankton did not reduce the standing crop of phytoplankton. The phytoplankton production rate averaged 5.5 times higher than biomass density. The correlation between grazer biomass and phytoplankton loss was low ($r = .03$).

Sinking rates of phytoplankton were estimated by comparing biomass peaks in the epilimnion with subsquent peaks in the hypolimnion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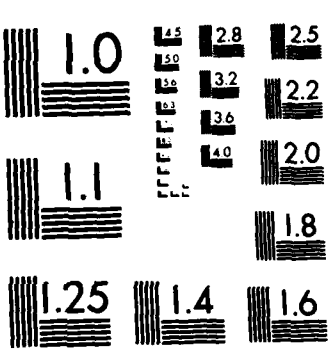

MICROCOPY RESOLUTION TEST CHART
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The average sinking rate was 0.76 m/day. This rate was multiplied by the phytoplankton biomass concentration in the hypolimnion to estimate phytoplankton loss to sinking which averaged 3.98 mgC/m^3/day. Phytoplankton loss through sinking was increased by turbidity during mixis but not during stratification. Phytoplankton lost from the epilimnion through sinking was 0.9% of the total loss.

The quantity of phytoplankton production recycled within the epilimnion was the remainder of the total loss after subtracting loss through grazing and sinking. An average of 89.6% of the phytoplankton production remained in the epilimnion and was recycled through death and bacterial decomposition. Total bacteria concentrations were largest in 1973 when phytoplankton recycling was six times larger than in 1974.

A production to chlorophyll ratio was used in 1974 to indicate whether biomass decreases were due to cell removal or to decreased efficiency of production. The ratio remained high when grazing losses were large, but low when losses were not due to grazing indicating that an environmental stress (low nutrients, temperature, light, etc.) was causing the losses.

Average grazer production in 1974 was estimated at 3.74 mgC/m^3/day. Energy transfer from phytoplankton to zooplankton was estimated at 15.5%. Grazer assimilation efficiency was 56%.

Instantaneous birth rates were calculated for Daphnia schodleri and Bosmina longirostris, the predominant grazers in 1974, and averaged 0.065 and 0.038, respectively. Birth rates of both species increased during pulses of diatoms, small-celled dinoflagellates, and green algae,

but D. schodleri birth rates did not respond to pulses of blue-green algae.

INTRODUCTION

Routes and magnitudes of primary production loss from the epilimnion during 1973 and 1974 were studied in Dworshak Reservoir. The dependence of zooplankton on primary production was also analyzed.

The following objectives were established for this study:

1. To determine the primary production, phytoplankton and zooplankton biomass, and phytoplankton loss rates over a period of two years.
2. To assess the effect of turbidity on primary production and phytoplankton loss rates.
3. To measure the degree to which zooplankton reduce phytoplankton biomass in the epilimnion through grazing.
4. To measure the amount of phytoplankton biomass which is lost to the hypolimnion through sinking.
5. To determine the amount of phytoplankton biomass which is recycled within the epilimnion through bacterial decomposition.
6. To determine the birth rate response of the major zooplankton genera to changes in the phytoplankton biomass and composition.

Researchers have been attempting to explain the processes underlying the rise and decline of phytoplankton populations for many years. Most of the initial research consisted of qualitative observations of temporal changes. Phytoplankton declines which coincided with zooplankton pulses were usually interpreted as a control of phytoplankton population size by the grazing activity of zooplankton. A few excellent reviews of temporal observation research summarized early works (Lund, 1965; Hutchinson, 1967).

Pennington (1941) using laboratory experiments was one of the first to observe that zooplankton in large concentrations can reduce the number of algae growing in a suspension. Since then much work has been published on the in vivo grazing and filtering rates of zooplankton (Ryther, 1954; Hall, 1964; Richman, 1958). Though valuable, this information is at best only a measure of potential grazing rates without the environmental variables of temperature, light, selectivity, competition, depth, etc. and their possible interactions.

More recently, research has turned to in situ grazing experiments to measure filtering and grazing rates. Techniques employ the use of radioactive tracers in phytoplankton, before and after grazing cell counts, and zooplankton gut content analyses to measure rates in the field (Dodson, 1974; Martin, 1970; Porter, 1972; and Welch et al., 1972).

Conclusions about the impact of grazing and the dependence of zooplankton on phytoplankton biomass vary considerably. Several investigations over the years have concluded that zooplankton grazing can account for all or most of the phytoplankton removal from the epilimnion. This conclusion has been reached through grazing experiments (Martin, 1970), productivity potential analysis (Wright, 1958), and zooplankton-phytoplankton trend correlations (Anderson et al., 1955).

The first major work which caused limnologists to doubt the ability of zooplankton to significantly reduce or control phytoplankton biomass was done on eutrophic Lake Erken, Sweden, by Nauwerck (1963). The study also placed doubt on the contention that zooplankton are solely dependent on phytoplankton as a food source. Nauwerck found that phytoplankton may often be of only secondary importance as a direct food source for

plankton. Dominant algal forms were diatoms, blue-greens, and small greens; dominant zooplankton genera were Daphnia sp., Bosmina sp., Ceriodaphnia sp., and Diaphanosoma sp. In situ filtering rate measurements showed that the zooplankton could not take up sufficient algae to account for their own substance production. Even if the whole primary production could be utilized it would hardly be sufficient. Filtration rates would have to be 10 to 100 times larger than those measured in order for grazers in Lake Erken to subsist. Nauwerck concluded that the levels of the trophic pyramid were often short-circuited, and a small addition from a lower level was sufficient to maintain the higher level. The most important food source for zooplankton was presumed to be bacteria and detrital products of phytoplankton decomposition.

A possible explanation for the contrasting conclusions about the effect of grazing on phytoplankton abundance is that phytoplankton production was seldom measured in conjunction with grazing rates and phytoplankton biomass. Since daily production is often much greater than biomass (Vollenweider, 1971), actual phytoplankton losses are probably much greater than observed biomass decreases usually associated with grazing. Recent work on lakes in the Cedar River Drainage, Washington, has combined measurements of phytoplankton production, algal biomass, and in situ zooplankton grazing rates (Welch et al., 1973). Results indicate that from one-half to six times the algal biomass can be removed by grazing per day, but the grazing rate was always less than the daily phytoplankton production.

This approach was expanded by Jassby and Goldman (1974) in a study on Castle Lake, California. Various routes of phytoplankton

production loss were investigated in their study. During most of the year grazing, combined with sinking, could not account for the loss of epilimnial phytoplankton production. Cell mortality and decomposition (recycling) accounted for the largest portion of phytoplankton production loss.

In this study algal biomass and algal production were used to determine the daily loss of phytoplankton. The technique is a modification of that used on Canyon Ferry Reservoir by Wright (1958). However, without grazing data or sinking rate data he was only able to convert his calculated loss data to grazing consumption and assume that all loss went to zooplankton. With in situ grazing experiments we directly measured the portion of algae lost to grazing. By measuring phytoplankton biomass in the photic zone and in the hypolimnion, loss through sinking could be determined. Having calculated total algal loss we were then able to calculate the amount of phytoplankton which is recycled within the epilimnion. By measuring total algal loss and then partitioning it into measureable routes of loss we were able to eliminate some of the assumptions often made by other investigators. Those assumptions were: 1) algal loss through sinking is insignificant during stratification (Wright, 1958); 2) decreases in phytoplankton biomass which coincide with increases in zooplankton biomass are attributable to grazing (Anderson et al., 1955); 3) changes in biomass reflect actual losses or increases in production (Martin, 1970); and 4) all phytoplankton loss goes to zooplankton, the next trophic level, during stratification (Wright, 1958).

DESCRIPTION OF THE RESERVOIR

Dworshak Reservoir is located on the North Fork of the Clearwater River in northern Idaho. The dam was built by the Army Corps of Engineers and the reservoir began filling in late 1971. Dworshak is 86 km (54 miles) long, with a surface area of 7122 hectares (17,600 acres), a depth of 192 m (630 feet), and a volume of 4.3×10^9 m^3 (3.5×10^6 acre-feet) at maximum pool level (Falter et al., 1977).

The North Fork Clearwater River drains a mountainous and forested watershed of 6.3×10^5 hectares (2440 sq. miles). The river flows through Columbia River basalt and exposed metamorphosed sediments of granite intrusions. The principle rocks exposed in the reservoir area include granite gneiss, granite, and basalt. Clay content in the soils is low to medium and silt content is medium to high. Surface soils in the area of the reservoir are, relatively, shallow (50-130 cm). The topography in the area is steep with slopes commonly between 40 and 70%.

The North Fork Clearwater River reaches a peak flow in mid-May of, approximately, 400-600 m^3/sec. Average annual flow is 100-200 m^3/sec. Two major tributaries to the reservoir are the Little North Fork River and Elk Creek.

Climate in the reservoir area is characterized by mild summers and long, cold winters with considerable snowfall. The annual precipitation near the dam averages 60 cm and increases with elevation in the upper reaches of the reservoir. The mean annual temperature at Orofino, Idaho, is 10 C with recorded extremes of 48 C and -31 C (U.S. Army Corps of Engineers, 1969).

METHODS

SAMPLE STATIONS

Two different parts of the reservoir were studied. One site was located 1.5 km upstream from the dam and designated as the main reservoir station. This was the deepest section of the reservoir (192 m) and was considered representative of the main body of the reservoir. The other site was in the Elk Creek Arm of the reservoir, at a point 6.5 km upstream from the main reservoir body. The Elk Creek Arm is the major arm on the reservoir and is 95 m deep at the study site. It was reasoned that the tributary area might develop different phytoplankton loss patterns than the main reservoir since its water quality was more similar to Elk Creek than the North Fork of the Clearwater River.

PHYTOPLANKTON

Sampling and Counting

Phytoplankton was sampled every 7 days in 1973 (March-November) and, approximately, every 5 days in 1974 at the main reservoir station. Samples were taken at 14 day intervals at Elk Creek Arm during 1973 and 1974.

Samples were collected at the surface, 3 m, 6 m, and 30 m with an 8-liter stainless steel Kemmerer bottle. A 1-liter bottle was filled from each depth and preserved with Lugol's solution. Samples were allowed to settle for 48 hrs. in glass settling chambers and the supernatant liquid siphoned off leaving, approximately, 60 ml of concentrated sample. A 1-ml aliquot was placed in a Sedgewick-Rafter cell and 10 to 100 fields were counted under 100X magnification.

Biomass Estimation

Phytoplankton biomass as carbon was determined from cell counts which were converted to cell volume and, subsequently, to cell weight by the following formula:

biomass = cell concentration x cell volume x carbon content

where biomass is expressed as mgC/m^3, cell concentration is $cells/m^3$, cell volume is mm^3/cell and carbon content is 0.10 mgC/mm^3. Mougeotia, Fragilaria, and Melosira were measured to calculate volume. Cell volumes of other genera were taken from the literature (Comita et al., 1959; Edmondson, 1971). Volume was converted to weight on the assumption that 1 mm^3 of phytoplankton has an ash-free dry weight of 0.20 mg (Hill et al., 1953). Ash-free dry weight is expressed as mgC/m^3 on the assumption that 50% of phytoplankton ash-free dry weight is carbon (Vollenweider, 1971). These conversions concur with the commonly used assumption that 10% of phytoplankton cell volume is carbon (Vollenweider, 1971).

Primary Production

Primary production was estimated at each station during 1973 and 1974 by the ^{14}C light- and dark-bottle method (USGS, 1973). Production was estimated at surface, 3 m, and 6 m depths from 4-hr midday incubations which coincided with phytoplankton sampling. Production measurements for a 4-hr period were expanded to production per day based on an 11-hr light day in December; a 12-hr day in March, April, September, October, and November; a 13-hr day in May and August; and a 14-hr day in June and July. Incubation period data was adjusted to a full day and expressed as production per day as suggested by the United States Geological Survey (1973).

Chlorophyll

Total chlorophyll was measured at the main reservoir station during 1974. One-liter samples were collected from the surface, 3 m, and 6 m depths using an 8-liter Kemmerer bottle. Sampling intervals coincided with the phytoplankton sampling dates. Total chlorphyll was determined within 8 hrs of collection by a spectrophotometric method for phytoplankton (USGS, 1973).

ZOOPLANKTON

Sampling and Counting

Zooplankton was sampled on the same dates when phytoplankton was sampled. A number 10 mesh net on a Miller sampler was towed to filter 1500-2000 l of water. Tows were made at 1 m and 10 m depths in 1973. Thirty three m to surface oblique tows were added in 1974. Samples were preserved in 10% formalin for later counting of 5-10 ml subsamples at 30X magnification. Average weight per animal was determined by drying 100 individuals of each genus on tared cover slips at 55 C for 12 hours then weighing to determine biomass (mgC/m^3).

Daphnia schodleri and Bosmina longirostris eggs were counted in all samples from the main reservoir station in 1974 for calculation of birth rates.

Grazing Rate Determination

Six in situ grazing experiments were conducted at the main reservoir station from June through August, 1973. These experiments follow the large volume plastic bag methods of Porter (1972). Clear polyethylene bags, 0.051 mm thick were used as grazing enclosures. The plastic

is non-toxic, inert, and highly permeable to oxygen and carbon dioxide (Porter, 1972). Two bags were pumped full with 40 l of water and suspended at the depth from which the water was pumped. Pairs of bags were suspended at 1 m, 5 m, and 20 m during each experiment. Pumping was done with a submersible electric water pump and plastic hose. Observations showed no obvious injury to the zooplankton from the pumping process. During each experiment one bag from each pair was filled with reservoir water containing the natural assemblage of phytoplankton and zooplankton. Water pumped into the second bag was filtered through 250 µm mesh net to remove grazers. This mesh size did not retain rotifers, copepod nauplii, or immature cladocerans and their eggs. Bags were suspended for a period of from 1.2-2.9 days. A pre- and post-experiment 1-liter sample was taken from each bag and preserved with Lugol's solution for later concentration and counting as with the other phytoplankton samples.

BACTERIA

Bacteria samples were collected at the surface in 1973 and 1974. Sampling from 12 m was included in 1974. Sampling coincided with phytoplankton sampling during both years. Bacteria samples were analyzed by Dr. Al Lingg, Bacteriology and Biochemistry Department, University of Idaho. Total counts were made on nutrient agar (Difco Laboratories, Detroit, Michigan) by the pour plate technique.

TEMPERATURE AND TURBIDITY

Temperature and turbidity were measured in conjunction with phytoplankton sampling. Temperature was measured with a bathythermograph or a digital read-out thermistor probe. Turbidity was measured with a Hach Model 2100A turbidimeter and recorded in formazin turbidity units

(FTU).

TOTAL PHYTOPLANKTON LOSS RATE CALCULATIONS

Biomass alone reveals little of phytoplankton community dynamics. In some lakes algal biomass may be as little as one tenth the algal production (Vollenweider, 1971). Standing crop is a balance between the rate of production and the rate of loss. Variations in standing crop depend upon factors which affect these rates.

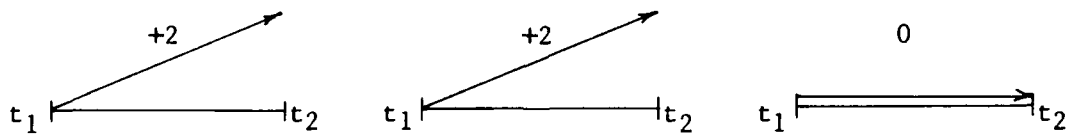
Phytoplankton loss (grazing, decomposition, and settling) can be thought of as that portion of production that does not remain as biomass. The average loss rates of phytoplankton during the intervals between successive sampling days were computed by the equation:

$$\langle L \rangle = \langle P \rangle - \langle dB/dt \rangle$$

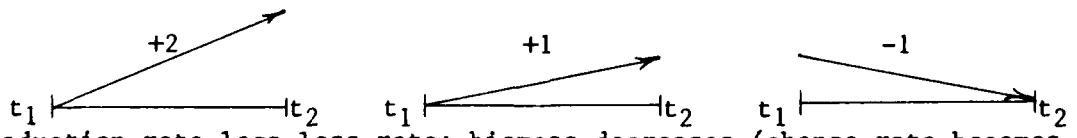
where L is the loss rate ($mgC/m^3/day$), P is the net primary production ($mgC/m^3/day$), B is the phytoplankton standing crop (mgC/m^3), t is time (days), and the carets indicate averages. The following examples express the relationship between loss, production, and biomass change rates:

LOSS RATE = PRODUCTION RATE - BIOMASS CHANGE RATE

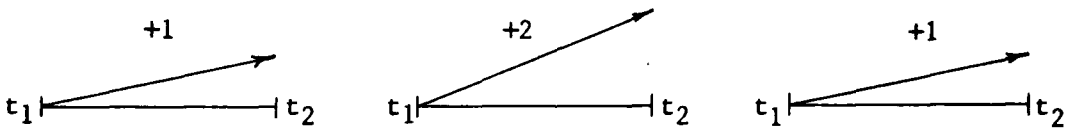
There are three possible conditions:



Loss rate equals production rate; biomass does not change.



Production rate lags loss rate; biomass decreases (change rate becomes negative).



Production rate exceeds loss rate and biomass increases (change rate becomes positive).

Net primary production, phytoplankton and zooplankton biomass, and epilimnial water temperatures and turbidities for each sample date (Tables 1, 2, 3, and 4) were used for calculations of phytoplankton loss rates from average biomass and average net primary production for the sample intervals listed in Tables 5, 6, and 7. Specific loss rates (mgC/mg phytoplankton C/day or day^{-1}) for each sample interval were estimated by dividing calculated loss rates (mgC/m^3/day) by the average biomass for the corresponding interval. Specific loss rates can be useful in comparing rates from one body of water to another since plankton concentrations per unit water volume may vary greatly. Tables 5, 6, and 7 also list grazer biomass and phytoplankton losses to grazing, sinking, and recycling and will be referred to throughout the text.

Net Production Rate (P)

Controversy has existed since the radioactive carbon method was first introduced over how close an approximation ^{14}C production is to net production. Recent work with ^{14}C production concludes that it is a very close approximation of net production. Bunt (1965) concluded from measurements of oxygen exchange and dark ^{14}C losses from labeled cells of Fragilaria sp. that ^{14}C uptake yields values of net photosynthesis. The view that ^{14}C uptake is a measure of net primary production is also supported by the work of Antia et al. (1963) and McAllister et al. (1964), in which the correspondence between the rate of ^{14}C uptake and the rate of

Table 1. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (main reservoir station), March-November, 1973.

Date	Average epilimnial temperature* (C)	Average epilimnial turbidity* (FTU)	Average epilimnial primary production* (mg C/m^3/day)	Average epilimnial phytoplankton biomass† (mg C/m^3)	Average epilimnial zooplankton biomass‡ (mg C/m^3)
March 8	6.1	--	10.70	31.00	7.47
April 4	7.3	2.7	1.55	143.54	7.92
April 22	6.4	--	1.35	103.64	101.06
May 4	9.7	4.2	61.04	91.44	83.09
May 10	9.6	--	25.28	101.22	30.16
May 18	15.4	--	26.31	58.08	160.60
May 24	13.9	--	276.39	80.18	232.99
May 31	15.6	2.5	146.09	13.41	188.22
June 7	14.7	4.3	76.01	5.63	205.37
June 14	15.2	2.6	51.84	13.25	143.84
June 22	--	--	--	40.98	57.06
June 28	20.7	2.0	80.24	--	66.62
July 4	20.3	1.2	40.05	12.44	59.46
July 12	19.6	2.0	11.85	6.39	203.46
July 19	--	1.7	15.89	9.26	23.69
July 29	--	2.7	239.07	18.66	9.71
August 2	23.6	1.2	207.57	7.82	2.45
August 9	20.3	2.3	--	13.94	8.59
August 30	19.7	0.7	--	--	131.98
September 6	18.4	2.0	133.23	38.20	66.05
September 22	17.6	1.7	350.14	199.55	101.35
October 4	15.9	4.6	--	19.56	26.06
October 18	13.5	2.6	178.72	3.45	16.13
October 27	--	6.3	115.86	.94	121.19
November 15	9.4	1.9	49.04	2.01	51.91
December 2	--	--	--	1.12	34.47
December 20	6.4	2.5	23.65	1.69	1.91
$\bar{x}$	14.5	2.6	96.45	40.70	79.36
s	5.3	1.34	98.58	51.62	71.09

*Average of surface, 3 m, 6 m, and 12 m depths.
†Average of surface, 3 m, and 6 m depths.
‡Average of 1 m and 10 m depths.

Table 2. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (main reservoir station), March-November, 1974.

Date	Average epilimnial temperature* (C)	Average epilimnial turbidity* (FTU)	Average epilimnial primary production* (mg C/m^3/day)	Average epilimnial phytoplankton biomass† (mg C/m^3)	Average epilimnial zooplankton biomass‡ (mg C/m^3)
March 13	3.3	9.2	16.22	1.68	.70
April 4	3.8	8.9	4.86	1.21	.52
May 7	10.1	7.6	112.02	24.97	2.04
May 14	9.9	—	84.29	13.91	.59
May 22	11.4	4.1	83.79	31.49	.59
May 28	9.9	3.4	37.00	13.28	2.27
June 4	10.9	3.2	119.66	11.38	—
June 7	13.8	—	106.75	9.06	8.97
June 13	13.8	3.1	30.32	7.38	13.87
June 17	11.7	0.2	174.80	4.39	—
June 20	13.6	–	110.26	2.42	61.49
June 25	12.7	2.5	37.38	.86	23.29
July 1	14.7	2.5	72.13	.15	94.32
July 4	16.3	—	55.27	.19	67.15
July 9	14.7	2.5	21.36	.15	174.08
July 16	14.7	1.6	30.73	.57	116.42
July 23	16.3	1.6	23.10	16.86	118.49
July 26	17.7	—	78.04	29.43	61.20
July 30	18.2	0.9	54.39	26.21	290.00
August 2	—	—	126.76	15.82	73.99
August 6	—	—	20.23	7.70	98.16
August 9	18.9	—	11.47	4.57	—
August 14	19.8	0.7	—	2.54	—
August 19	19.3	1.2	10.14	.88	132.23
August 27	19.2	1.8	15.95	.13	103.71
August 30	—	—	38.92	.13	143.97
September 5	17.7	1.9	24.35	—	97.60
September 20	17.2	0.7	18.18	1.55	36.44
October 3	15.4	—	11.39	15.66	36.40
October 8	14.4	2.7	26.29	15.24	21.41
October 29	12.3	—	110.39	9.16	21.92
November 22	9.7	1.9	134.30	3.17	12.27
$\bar{x}$	13.8	3.0	58.10	8.78	64.79
s	4.2	2.55	46.25	9.38	67.65

*Average of surface, 3 m, 6 m, and 12 m depths.
†Average of surface, 3 m, and 6 m depths.
‡Average of 1 m and 10 m depths.

Table 3. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (Elk Creek Arm station), March-November, 1973.

Date	Average epilimnial temperature* (C)	Average epilimnial turbidity* (FTU)	Average epilimnial primary production* (ıg C/m^3/day)	Average epilimnial phytoplankton biomass† (mg C/m^3)	Average epilimnial zooplankton biomass‡ (mg C/m^3)
March 9	5.6	1.9	33.43	3.83	1.84
April 5	6.3	2.7	4.46	36.73	4.24
May 5	9.5	4.7	204.78	63.12	4.69
May 19	13.3	—	51.20	41.71	219.77
June 1	15.9	—	104.73	16.56	373.42
June 8	14.3	3.1	43.73	15.46	176.63
June 22	—	—	—	73.93	168.37
July 5	18.4	2.1	—	12.05	136.19
July 12	16.6	2.0	26.59	8.40	116.31
July 27	21.2	2.2	409.91	4.67	32.96
August 9	20.3	2.4	—	19.78	21.78
August 24	19.8	1.5	—	—	14.98
September 7	18.4	1.7	344.66	49.56	41.20
September 21	17.3	1.3	503.52	44.67	91.04
October 12	12.8	3.9	123.04	4.31	8.32
October 28	—	5.0	—	3.08	58.23
November 16	9.2	2.0	472.22	1.95	13.70
December 3	—	—	—	1.82	13.51
December 21	6.3	3.9	67.67	1.24	7.15
$\bar{x}$	14.1	2.7	190.00	22.38	79.17
s	5.3	1.13	181.71	23.22	98.87

*Average of surface, 3 m, 6 m, and 12 m depths.
†Average of surface, 3 m, and 6 m depths.
‡Average of 1 m and 10 m depths.

Table 4. Average epilimnial water temperature, turbidity, primary production, phytoplankton biomass, and zooplankton biomass in Dworshak Reservoir (Elk Creek Arm station), March-November, 1974.

Date	Average epilimnial temperature* (C)	Average epilimnial turbidity* (FTU)	Average epilimnial primary production* (mg C/m^3/day)	Average epilimnial phytoplankton biomass† (mg C/m^3)	Average epilimnial zooplankton biomass‡ (mg C/m^3)
March 14	2.9	24.5	4.62	2.50	1.79
April 3	3.9	9.5	24.99	1.97	3.21
May 8	8.5	7.7	10.51	1.91	.07
May 23	—	5.7	29.38	7.16	.28
June 11	12.9	—	154.57	9.21	12.09
June 26	—	5.9	68.70	1.53	20.20
July 12	15.2	2.5	116.24	.46	275.69
July 22	—	2.6	6.58	14.56	237.20
August 7	17.9	1.7	10.69	1.74	79.86
August 20	—	1.2	11.40	1.06	78.11
September 5	17.9	—	50.29	—	55.61
September 19	—	1.5	21.28	2.07	83.57
October 8	12.7	1.8	47.69	4.99	4.07
November 19	9.4	1.9	384.64	.20	10.09
$\bar{x}$	11.3	5.5	67.25	3.80	61.56
s	5.5	6.57	101.49	4.19	88.78

*Average of surface, 3 m, 6 m, and 12 m depths.
†Average of surface, 3 m, and 6 m depths.
‡Average of 1 m and 10 m depths.

Table 5. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (main reservoir station), March-December, 1973.

Date	Average epilimnial phytoplankton biomass (mg C/m^3)	Average net primary production (mg C/m^3/day)	Average specific loss rate (day^{-1})	Average phytoplankton loss rate (mg C/m^3/day)	Average grazer biomass (mg C/m^3)	Average phytoplankton loss to grazing (mg C/m^3/day)	Average phytoplankton loss to sinking (mg C/m^3/day)	Average phytoplankton loss recycled within epilimnion (mg C/m^3/day)
3/8-4/4	87.267	6.125	0.130	11.345	7.695	9.596	12.581	0
4/4-4/22	71.768	1.450	0.030	2.153	54.489	55.882*	0.580	0
4/22-5/4	97.537	31.199	0.350	34.138	92.075	128.334*	1.096	0
5/4-5/10	96.331	43.159	0.441	42.482	56.625	77.948*	2.012	0
5/10-5/18	79.654	25.794	0.419	33.375	95.378	108.565*	6.283	0
5/18-5/24	69.130	151.349	1.897	131.140	196.794	194.406*	12.926	0
5/24-5/31	46.795	211.238	7.373	345.019	210.607	140.833	22.490	181.696
5/31-6/7	9.522	111.047	12.313	117.244	196.797	26.778	19.517	70.949
6/7-6/14	9.440	63.921	8.591	81.099	174.606	23.554	–	57.545
6/14-6/22	27.115	–	–	–	100.449	38.921	8.809	–
6/22-6/28	–	66.038	–	–	61.838	–	–	–
6/28-7/4	26.710	60.147	3.655	97.625	63.041	24.062	5.435	68.128
7/4-7/12	9.417	25.951	2.617	24.644	131.462	17.691	2.124	4.829
7/12-7/19	7.827	13.869	1.733	13.564	113.574	12.703	0.865	0
7/19-7/26	13.961	127.479	7.167	100.058	16.699	3.331	0.544	96.183
7/26-8/2	13.241	223.317	19.789	262.026	6.080	1.150	0.526	260.350
8/2-8/9	10.882	–	–	–	5.517	0.858	0.777	–
8/9-8/30	–	–	–	–	70.282	–	–	–
8/30-9/6	26.071	170.397	14.977	390.465	99.015	36.888	1.675	351.902
9/6-9/22	118.873	241.684	2.537	301.581	83.703	142.186	2.301	157.094
9/22-10/4	109.553	–	–	–	63.707	99.734	4.908	–
10/4-10/18	11.504	264.428	26.886	309.297	21.097	3.468	4.702	301.127
10/18-10/27	2.196	147.290	87.469	192.082	68.661	2.155	1.266	188.661
10/27-11/15	1.477	82.452	73.594	108.698	86.551	1.827	0.382	106.489
11/15-12/2	1.565	–	–	–	43.191	0.966	0.240	–
12/2-12/20	1.403	36.347	19.187	26.919	18.189	0.365	0.331	26.223

*Calculated loss to grazing is equal to or greater than total loss.

Table 6. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (main reservoir station), March-December, 1974.

Date	Average epilimnial phytoplankton biomass (mg C/m^3)	Average net primary production (mg C/m^3/day)	Average specific loss rate (day^{-1})	Average phytoplankton loss rate (mg C/m^3/day)	Average grazer biomass (mg C/m^3)	Average phytoplankton loss to grazing (mg C/m^3/day)	Average phytoplankton loss to sinking (mg C/m^3/day)	Average phytoplankton loss recycled within epilimnion (mg C/m^3/day)
3/13-4/4	1.450	10.542	6.832	9.903	.614	.013	0.802	9.088
4/4-5/7	13.095	58.441	4.188	54.842	6.340	1.186	0.639	53.017
5/7-5/14	19.442	98.157	5.354	104.092	1.317	.366	0.678	103.048
5/14-5/22	22.697	84.039	4.264	96.782	.592	.192	0.497	96.093
5/22-5/28	22.381	60.391	2.860	63.709	1.433	.458	0.440	62.811
5/28-6/4	12.327	78.328	6.674	82.270	5.625	.991	0.457	80.822
6/4-6/7	10.219	113.204	11.226	114.718	5.625	.821	0.749	113.148
6/7-6/13	8.221	68.537	7.979	65.591	11.425	1.342	0.617	63.632
6/13-6/17	5.887	102.564	22.076	129.961	37.685	3.170	0.815	125.976
6/17-6/20	3.408	142.534	42.842	146.005	37.685	1.835	0.817	143.353
6/20-6/25	1.640	73.822	44.753	73.395	42.391	.993	0.824	71.578
6/25-7/1	.501	54.754	269.058	134.932	58.802	.421	0.492	134.019
7/1-7/4	.167	63.700	393.929	65.786	80.735	.193	0.160	65.433
7/4-7/9	.169	38.318	218.258	36.886	120.616	.291	0.039	36.556
7/9-7/16	.361	26.047	97.908	35.345	145.247	.749	0.036	34.560
7/16-7/23	8.715	26.915	27.547	240.058	117.453	14.627	0.067	225.364
7/23-7/26	23.143	50.568	1.830	42.351	89.842	29.712	0.102	12.537
7/26-7/30	27.821	66.213	2.392	66.547	175.597	69.811*	0.084	0
7/30-8/2	21.015	90.577	5.210	109.485	181.995	54.654	0.084	54.747
8/2-8/6	11.758	73.495	5.494	64.598	86.077	14.463	0.175	49.960
8/6-8/9	6.137	15.847	2.737	16.797	115.193	10.102	0.175	6.520
8/14-8/19	1.711	10.803	7.196	12.309	117.967	2.884	0.128	9.297
8/19-8/27	.507	13.045	65.899	33.444	123.840	.897	0.196	32.351
8/27-8/30	.132	27.437	208.528	27.526	92.668	.175	0.305	27.046
8/30-9/20	.841	27.150	154.335	129.873	92.668	1.114	0.112	128.647
9/20-10/3	8.607	14.784	6.095	52.463	36.417	4.479	0.101	47.883
10/3-10/8	15.451	18.840	1.231	19.021	28.902	6.381	0.191	12.449
10/8-10/29	12.201	68.340	6.911	84.321	21.665	3.777	0.581	79.963
10/29-11/22	6.167	122.346	27.241	167.982	17.096	1.507	1.609	164.866

*Calculated loss to grazing is equal to or greater than total loss.

Table 7. Calculation of phytoplankton loss from the epilimnion in Dworshak Reservoir (Elk Creek Arm station), March-December, 1973 and 1974.

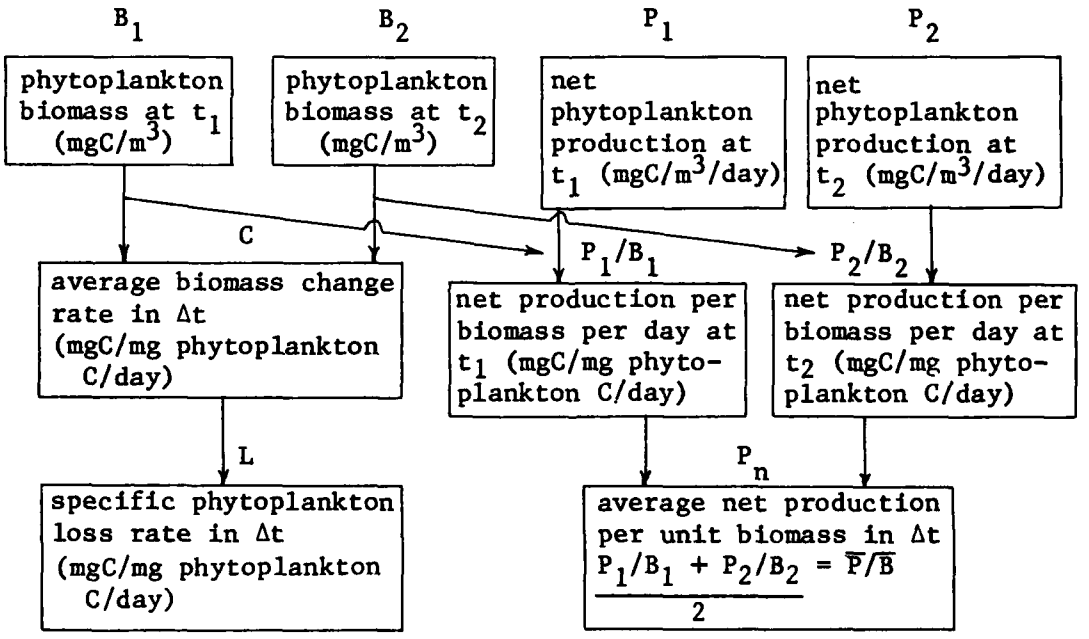
Date	Average epilimnial phytoplankton biomass (mg C/m^3)	Average net primary production (mg C/m^3/day)	Average specific loss rate (day^{-1})	Average phytoplankton loss rate (mg C/m^3/day)	Average grazer biomass (mg C/m^3)	Average phytoplankton loss to grazing (mg C/m^3/day)	Average phytoplankton loss to sinking (mg C/m^3/day)	Average phytoplankton loss recycled within epilimnion (mg C/m^3/day)
1973								
3/9-4/5	20.280	18.943	4.362	88.461	3.040	0.881	0.894	86.686
4/5-5/5	49.922	104.617	1.664	83.070	4.464	3.185	5.755	74.130
5/5-5/19	52.414	127.987	2.265	118.718	112.233	84.062	5.737	28.919
5/19-6/1	29.137	117.964	6.257	182.310	296.595	123.492	12.072	46.746
6/1-6/8	16.011	114.231	7.001	112.093	274.525	62.810	18.916	30.367
6/8-6/22	44.696	–	–	–	172.002	109.859	9.720	–
6/22-7/5	42.991	–	–	–	152.279	93.551	4.275	–
7/5-7/12	10.223	35.163	3.077	31.456	126.249	18.443	2.704	10.309
7/12-7/27	6.535	218.255	45.463	297.101	74.633	6.970	1.045	289.086
7/27-8/9	12.229	–	–	–	27.367	4.782	1.377	–
8/9-8/24	–	–	–	–	18.381	–	–	–
8/24-9/7	34.669	377.289	47.373	1642.375	28.093	13.918	2.372	1626.085
9/7-9/21	47.111	424.093	9.121	429.699	66.123	44.515	3.083	382.101
9/21-10/12	24.490	131.280	19.978	489.261	49.681	17.386	1.997	469.878
10/12-10/28	3.699	–	–	–	33.275	1.759	0.646	–
10/28-11/16	2.517	297.626	135.327	340.618	35.966	1.294	0.470	338.854
11/16-12/3	1.883	–	–	–	13.606	0.366	0.494	–
12/3-12/21	1.527	269.942	148.351	226.532	10.333	0.225	1.094	225.213
1974								
3/14-4/3	2.235	14.806	7.283	16.277	2.499	0.080	2.074	14.123
4/3-5/8	1.939	17.753	9.099	17.643	1.637	0.045	2.333	15.265
5/8-5/23	4.537	19.949	4.726	21.442	0.175	0.011	2.394	19.037
5/23-6/11	8.187	91.975	10.429	85.382	6.189	0.724	1.099	84.211
6/11-6/26	5.367	111.631	31.010	166.431	16.147	1.238	0.819	164.374
6/26-7/12	.991	92.467	149.765	148.417	147.943	2.095	0.380	145.942
7/12-7/22	7.507	61.409	127.212	954.980	256.443	27.510	0.239	927.231
7/22-8/7	8.149	8.635	3.393	27.649	158.528	18.460	0.919	8.270
8/7-8/20	1.401	11.045	8.489	11.893	78.981	1.581	1.265	9.047
8/20-9/5	–	30.844	–	–	66.859	–	–	–
9/5-9/19	1.565	35.782	10.508	16.445	69.593	1.556	0.617	14.272
9/19-10/8	3.531	34.482	9.871	34.885	43.819	2.211	0.223	32.421
10/8-11/19	2.597	–	–	–	7.079	0.263	0.212	–

increase of cell carbon was actually observed. Therefore, we concluded that the rate of phytosynthesis as measured by the carbon-14 technique in this study could be accepted as the rate of phytoplankton net production.

Biomass Change Rate (C)

The rate of biomass change per unit weight of biomass was calculated by dividing the difference between biomass values on two successive dates by the average biomass for the two days and then dividing this quotient by the number of days between the dates. Actual total phytoplankton loss in $mgC/m^3/day$ was calculated as average loss rate times average biomass for each sample period (Column 4, Tables 5, 6, and 7).

Specific phytoplankton loss calculated from production and biomass data is illustrated in the following diagram:



GRAZING RATE DETERMINATION

Fragilaria was chosen as the genus best suited for in situ measurement of zooplankton grazing rates in Dworshak. It was the algal form that was consistantly abundant throughout the months of thermal stratification. Fragilaria is a form small enough to be grazed by most zooplankton in Dworshak yet large enough to represent most of the algal forms present. Only 14% of all cells sampled in 1974 were larger than Fragilaria. It is also a good form for experimentation since it does not float like blue-greens nor tangle and sink as do long filamentous forms like Mougeotia. Fragilaria was the only algal form present during all six experiments and averaged 70% of the phytoplankton biomass throughout the experiments.

The depths of 1 m, 5 m, and 20 m were chosen as experimental depths to determine which depth provided optimum temperature and light for measuring grazing rates. The major problem encountered in confining phytoplankton was an increase in production within the enclosure. This problem was also encountered in phytoplankton bioassays in Dworshak (Stowell, 1976) and in other bodies of water (Porter, 1972). The increased production appears to be a response to light or temperature since algae suspended at 20 m did not exhibit increased production. The results of the July 3-5, 1973 grazing experiment demonstrate this phenomenon (Table 8).

Grazing that may be occurring at 1 m and 5 m is difficult to detect and separate from the increased rate of production. Increased production adds variation and tends to mask differences in treatments due to grazing.

Only the results of the grazing experiments at 20 m were used to calculate grazing rates. A randomized block design was used to analyze treatment effects. Each experiment was a block and the bag enclosures

Table 8. *Fragilaria* cell counts in grazing enclosures with and without zooplankton during July 3-5, 1973 in Dworshak Reservoir.

Treatment	Rep.	Depth 1 m	5 m	20 m
Initial cell counts (*Fragilaria* cells/l)	1	75,492	74,453	57,985
	2	61,560	98,128	70,992
Final cell counts zooplankton absent	1	522,498	161,280	70,862
	2	453,866	240,192	—
Final cell counts zooplankton present	1	404,186	45,057	32,061
	2	494,172	78,818	60,912

(with and without zooplankton) were treatments. Results indicate a significant difference between treatments at the 79% ($P \leq 0.21$) level of significance (Table 9).

The reason for the difficulty in detecting a difference (assuming that a difference exists) may be that Dworshak Reservoir water is not as eutrophic as waters where this procedure has been used successfully. Porter (1972), who developed the polyethylene bag technique, worked with water which had 5-7 million cells/l. She determined that in order to detect treatment differences a minimum of 5000 cells must be counted per sample or all cells in, approximately, 1.5 ml of water.

Dworshak Fragilaria concentrations ranged from, approximately, 2000-150,000 cells/l during the six experiments. Consequently, all cells in 33-2500 ml of water would have had to been counted in order to detect a significant treatment difference at the 95% ($P \leq 0.05$) level.

Since Fragilaria cells were reduced in the presence of zooplankton in five of the six experiments the average difference in treatments was used to calculate a zooplankton community filtering rate. The grazing rate based on these in situ experiments can be more accurately applied to Dworshak Reservoir in calculating grazing losses than grazing rates determined in studies on other bodies of water or filtering rates determined in laboratory experiments.

The grazing rates (mg Fragilaria carbon/mg zooplankton C/day) for each experiment were converted to a filtering rate by dividing by the concentration of Fragilaria (mgC/m^3) in each experiment. The average filtering rate for all experiments was then used to calculate phytoplankton biomass lost to grazing for each sample interval.

Table 9. Calculation of zooplankton grazing rates on *Fragilaria* at 20 m from six *in situ* measurements in Dworshak Reservoir, 1973. (June 22, July 3, and July 17 numbers are an average of 2 replicates; numbers during other dates represent only 1 replicate.)

	June 22	July 3	July 17	July 25	August 4	August 28	Means
Duration of measurement (days)	1.25	2.92	2.04	2.08	2.29	2.00	2.09
Initial (cells/l)	156,127	64,488	8,512	55,281	171,739	1,759	76,317.7
Final-zooplankton absent (cells/l)	70,785	70,862	5,210	89,902	117,089	1,946	59,299.0
Final-zooplankton present (cells/l)	61,695	46,486	19,530	49,748	109,109	0	47,761.3*
Grazing loss: cells/l	9,090	24,376	0	40,154	7,980	1,946	13,924.3
mg C/m^3	.295	.790	0	1.301	.259	.063	.451
mg C/m^3/day	.236	.271	0	.625	.113	.031	.212
mg zooplankton C/m^3 (10 m)†	85.945	109.194	40.610	12.448	13.967	138.322	66.748
mg phytoplankton C/mg zooplankton C/day	.00275	.00248	0	.05021	.00809	.00022	.01063
m^3/mg zooplankton C/day	.00932	.00314	0	.03859	.03123	.00349	.01429
Percent of total biomass represented by *Fragilaria*	71	95	59	76	97	23	70

* A significant difference between treatment effect ($P \leq .21$; $P \leq .13$ without July 17 data) as determined by a randomized complete-block design ANOVA.

† *Polyphemus* sp. not included since it is considered a non-grazer (Pennak, 1953).

SINKING RATE DETERMINATION

Phytoplankton biomass was measured at the surface, 3 m, and 6 m in the epilimnion. Biomass at these depths were averaged and are assumed to represent the biomass of the epilimnion. The thermocline varied from a depth of nine meters during early stratification to 18 m just before mixis. During each sampling period phytoplankton biomass was measured at 30 m, a depth which was always below the thermocline. An estimate of the portion of algal biomass lost from the epilimnion through sinking was made by comparing phytoplankton biomass at 30 m with the average biomass within the epilimnion.

RESULTS AND DISCUSSION

There are three major routes of phytoplankton loss in Dworshak Reservoir. Production not remaining in the epilimnion as standing crop can either be routed to the next trophic level (zooplankton), sink out of the euphotic zone, or be recycled within the epilimnion through death and bacterial decomposition. Of course, all loss may eventually be recycled but this study is primarily concerned with the immediate loss of production and subsequent routing during stratification.

Horizontal transport can be a route of loss in flow-through lakes and reservoirs (Jassby et al., 1974). Dworshak is not considered to be a flow-through system because of its great depth and volume in relation to the quantity of water moving through it. Also, since most water is drawn off from below the epilimnion, horizontal transport is not considered to be an important phytoplankton loss route.

PHYTOPLANKTON LOSS THROUGH GRAZING

Grazing Coefficient

The average grazing rate over all experiments was 0.0106 mg phytoplankton carbon/mg zooplankton carbon/day. This ingestion rate is based on total zooplankton biomass minus *Polyphemus pediculus* biomass. *P. pediculus* was the only species in Dworshak known to be strictly predaceous, feeding on other Entomostraca and rotifers. *Cyclops bicuspidatus thomasi* is not a true filter feeder but since its food consists of unicellular algae and animals it was included with the grazer biomass (Pennak, 1953). The average filtering rate for the six experiments was 0.01429 m^3/mg zooplankton C/day (Table 9).

The average filtering rate, or grazing coefficient as it has been termed by Wright (1965), is higher in Dworshak than rates in other studies. However, there was a lack of data on grazing coefficients for entire zooplankton communities and limited data on rates for all genera of grazers. Richman (1958) determined that Daphnia filter 0.00281 to 0.00468 m^3/mg zooplankton C/day depending on the size of the animals. Wright (1965) estimated the coefficient to be 0.00272 m^3/mg zooplankton C/day in Canyon Ferry Reservoir, Montana. This was a coefficient based on the entire community where Daphnia was the predominant genus present. Burns and Rigler (1967) determined the grazing coefficient for Daphnia rosea in natural lake water to be 0.00164 m^3/mg zooplankton C/day.

Laboratory and field experiments indicate a straight-line relationship between filtering rate and size of zooplankton. Smaller animals filter at a faster rate per unit body weight than large grazers (Ryther, 1954; Richman, 1958). Bosmina, for example, a relatively small form, filtered at a rate of 0.0114 m^3/mgC/day (Jassby et al., 1974). This size to filtering rate relationship may explain the higher grazing coefficient in Dworshak since the reservoir has large concentrations of Bosmina longirostris (0.004 mg body weight/individual) and Cyclops bicuspidatus thomasi (0.007 mg body weight/individual); both smaller than Daphnia longirostris (0.014 mg body weight/individual). Concentrations of Ceriodaphnia reticulata (0.006 mg body weight/individual) and Holopedium gibberum (0.024 mg body weight/individual) were low in Dworshak.

Grazing Losses

Grazing loss for each sample period was calculated from the experimentally determined filtering rate by multiplying filtering rate (m^3/mg

zooplankton C/day) times the average epilimnial phytoplankton concentration (mg phytoplankton C/m^3) and then multiplying the product by the average epilimnial zooplankton concentration (mg zooplankton C/m^3) (Column 6, Tables 5, 6, and 7).

Grazing losses must be viewed as only a potential maximum estimate since it is assumed that all algae are grazed by all grazers and at the same rate. This assumption does not hold true in some cases, for example, large algal forms like Dinobryon and Staurastrum are probably grazed by only a few large zooplankton and at a much slower rate than small diatoms.

Phytoplankton losses to grazing at both sample stations throughout 1973 and 1974 ranged from less than one to 194.4 mgC/m^3/day. The overall average was 24.7 mgC/m^3/day. These grazing losses compare with 57.5 mgC/m^3/day obtained by Wright in Canyon Ferry Reservoir. Canyon Ferry was only studied during September and October when grazing was estimated to be at a peak (Wright, 1958).

The average annual values of grazing loss were 48.0 and 34.5 mgC/m^3/day in the main reservoir and Elk Creek Arm, respectively, in 1973. Average grazing losses were 7.8 and 4.6 mgC/m^3/day in the main reservoir and Elk Creek Arm, respectively, in 1974 or an average decrease of 85% in grazing loss from 1973 to 1974 (Tables 5, 6, and 7).

The decrease in grazing loss from 1973 to 1974 coincided with an increase in spring turbidity (Figures 1 and 2). During both years grazing losses reached a mid-summer high of about 30 to 40% of the total phytoplankton loss in July and August. Grazing made up a relatively small percentage of total phytoplankton loss during the late summer and fall. The spring of 1973 was a time of high production and high loss to grazing.

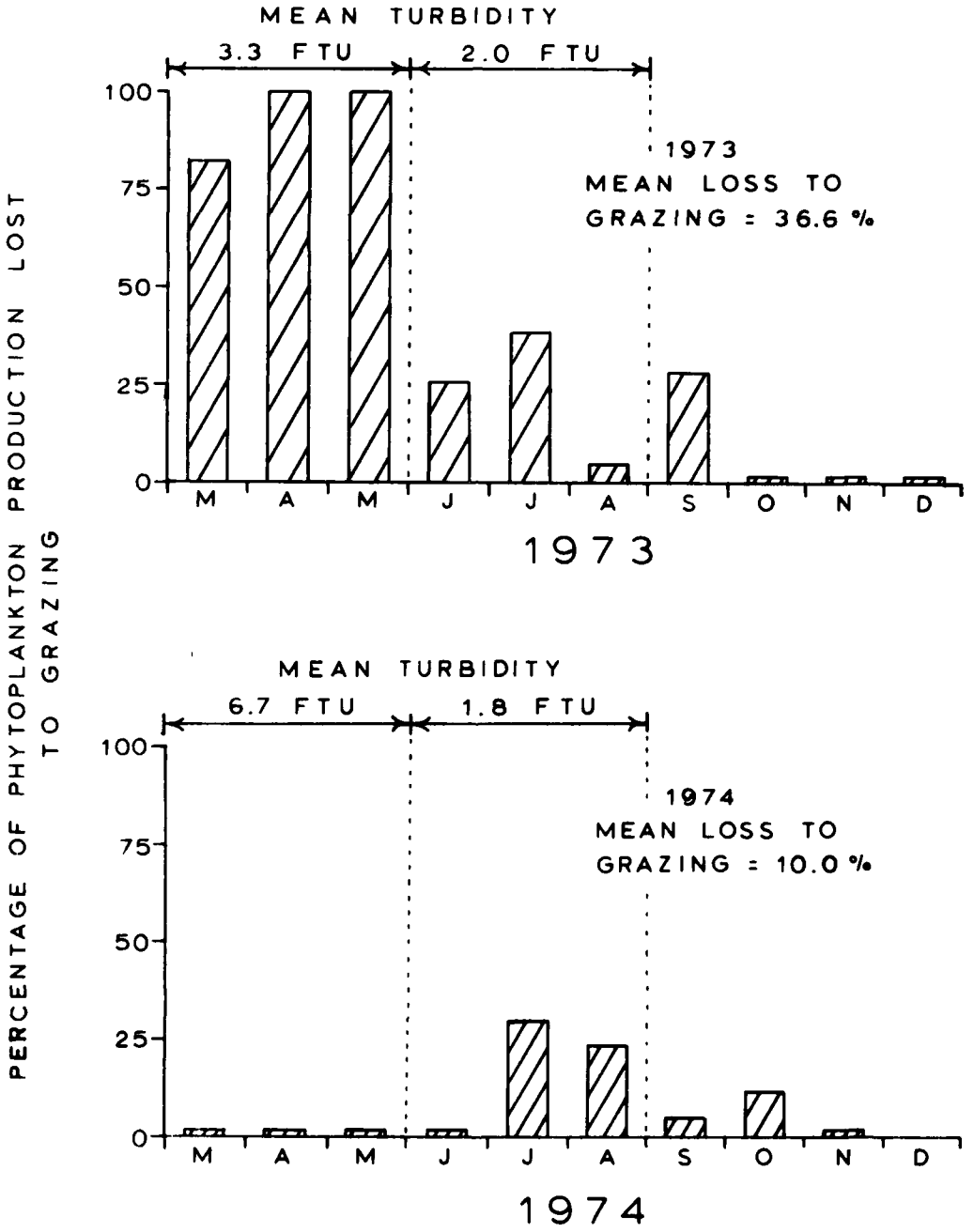


Figure 1. Relationship of spring and summer turbidity with monthly average percentage of phytoplankton loss to zooplankton grazing in Dworshak Reservoir (main reservoir station), 1973 and 1974 (FTU = formazin turbidity units).

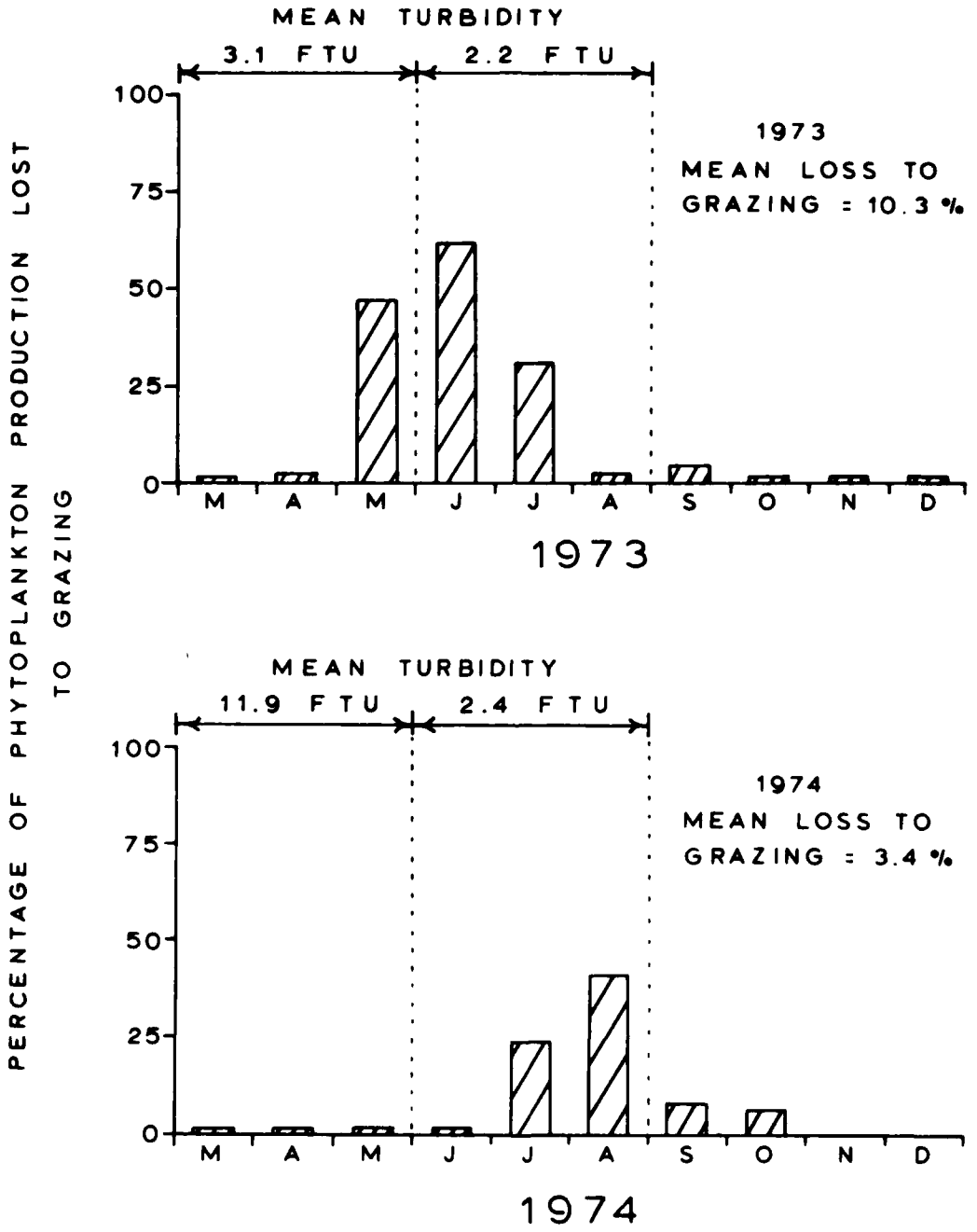


Figure 2. Relationship of spring and summer turbidity with monthly average percentage of phytoplankton loss to zooplankton grazing in Dworshak Reservoir (Elk Creek Arm), 1973 and 1974 (FTU = formazin turbidity units).

The spring of 1974 was a period of extremely low grazing loss even though production remained nearly the same as in 1973. It appears that grazing was reduced by increased turbidity.

Several inferences about grazer preferences or selectivity can be made by comparing phytoplankton biomass and grazing loss throughout each year (Figures 3 and 4). However, loss to grazing was calculated by using phytoplankton biomass as a variable and the two parameters should not be compared via correlational techniques. Phytoplankton biomass and loss to grazing followed similar trends at the main reservoir and Elk Creek Arm stations during 1973 and 1974. Spring phytoplankton biomass (mostly diatoms) peaked earlier in the main reservoir than in Elk Creek Arm in 1973. These peaks were followed closely by large zooplankton populations (Daphnia schodleri and Cyclops bicuspidatus thomasi) during April and May, 1973. Grazing losses reached a peak throughout the reservoir as diatom concentrations decreased sharply in May. Diatoms and green algae peaked again at both sample areas in June and grazing losses were high. D. schodleri and C. bicuspidatus thomasi were abundant at that time. Both biomass and grazing were low through most of July and August, 1973. Biomass peaked in September due to a bloom of green algae. This bloom coincided with a large grazing loss and increased abundance of D. schodleri. Biomass and grazing loss were very low in the late fall and winter months. These 1973 trends indicate that spring diatoms may be utilized by C. bicuspidatus thomasi and D. schodleri and mid-summer diatoms and green algae may be grazed by D. schodleri and C. bicuspidatus thomasi. Staurastrum was the green algae that contributed to high grazing losses. D. schodleri was the predominant grazer present during September but it

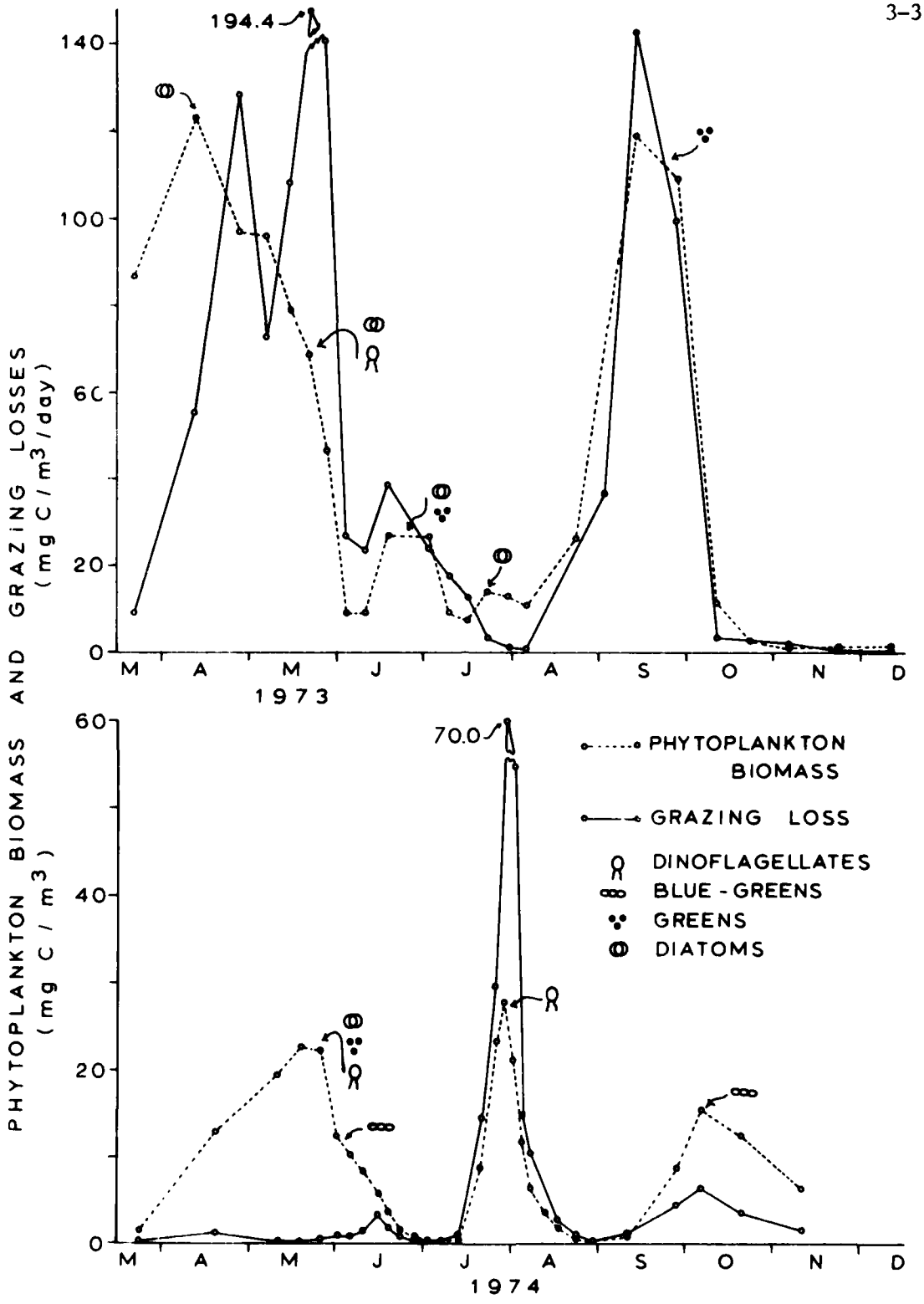


Figure 3. Epilimnial phytoplankton biomass, composition, and loss to grazing in Dworshak Reservoir (main reservoir station), 1973 and 1974.

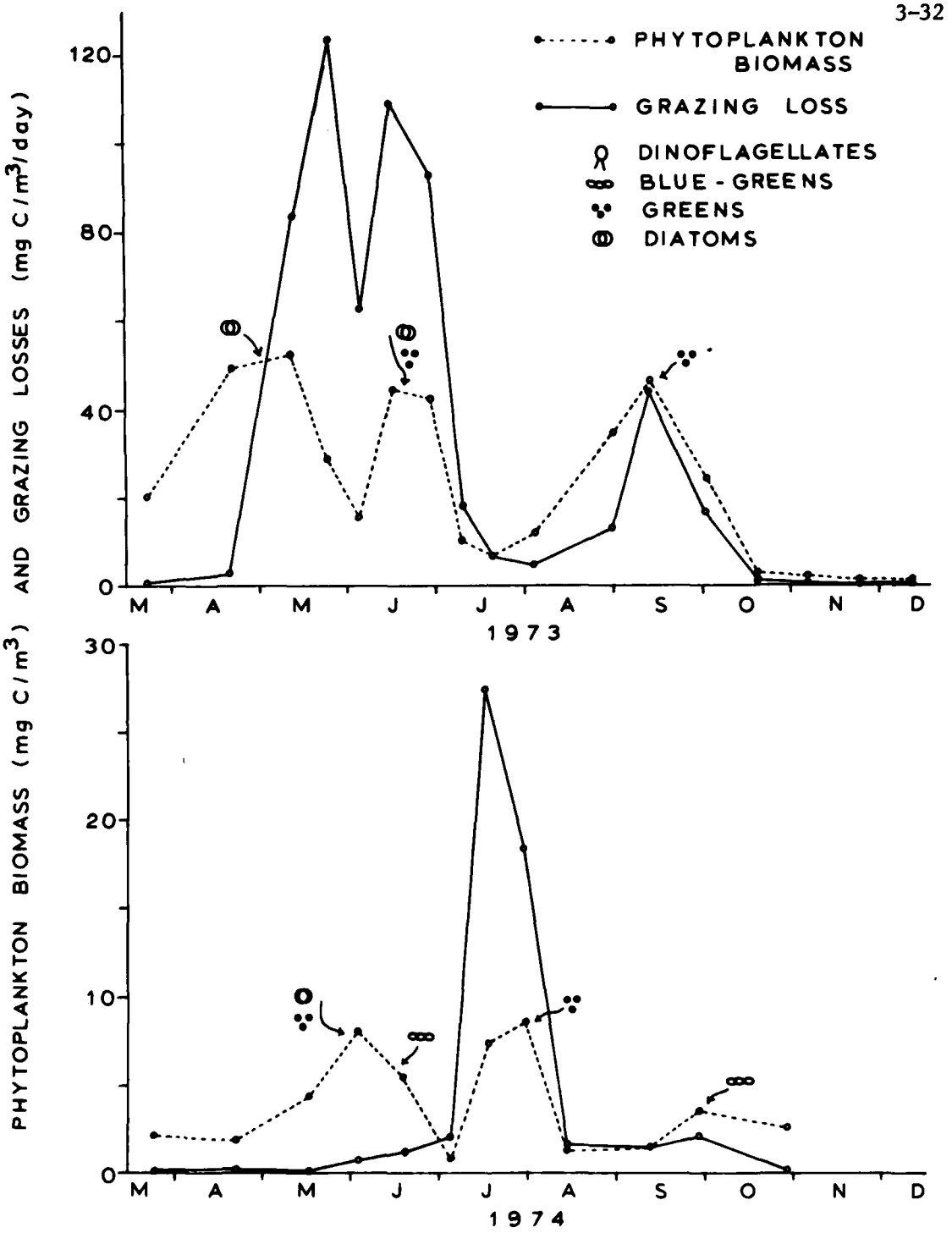


Figure 4. Epilimnial phytoplankton biomass, composition, and loss to grazing in Dworshak Reservoir (Elk Creek Arm), 1973 and 1974.

seems unlikely that it could remove a large form like Staurastrum at a noticeable rate.

Biomass and grazing trends were much different in 1974 due to the increased spring turbidity. Spring diatom pulses mixed with greens and blue-greens peaked, approximately, one month later at both sample areas and were of much smaller magnitude than in 1973. Zooplankton numbers and resulting grazing losses did not reach significant levels until mid-summer. In the main reservoir the mid-summer phytoplankton biomass peak consisted of a small-celled dinoflagellate (Dinobryon) bloom. This bloom coincided with large grazing losses and populations of D. schodleri and Bosmina longirostris. In the Elk Creek arm green algae peaked in July coinciding with high grazing losses and the presence of D. schodleri and C. bicuspidatus thomasi. The fall phytoplankton biomass in both parts of the reservoir was predominantly blue-greens (Anabaena and Aphanizomenon) which peaked in early October. The grazing losses were of relatively low magnitude during that time. The predominant grazer during the fall was a population of Ceriodaphnia reticulata.

The occurrence of an inverse relationship between phytoplankton and zooplankton can give strong presumptive evidence that grazing is a major factor in phytoplankton loss. This relationship, however, only exists in waters where production is not much greater than the standing crop; a condition where the "surplus production" may be grazed entirely and thus the biomass can diminish. In oligotrophic lakes zooplankton can utilize much or all of the production and reduce the standing crop (Edmondson, 1957; Hutchinson, 1967; Welch et al., 1973). Since production was larger than standing crop in Dworshak during stratification (Tables 1, 2, 3, and

4), grazing only removed a small percentage of the production; zooplankton, therefore, did not control phytoplankton numbers. The inverse relationship between phyto- and zooplankton biomass was not apparent.

There also appears to be no obvious relationship between zooplankton biomass and phytoplankton loss rates in Dworshak. Wright (1956) found a high correlation (r = .969) between these parameters in oligotrophic waters where zooplankton removed 72.6% of the primary production. Zooplankton removed only 9.5% of the primary production in Dworshak and as might be expected in these more eutrophic waters the correlation coefficient between grazer biomass and phytoplankton loss was only .03.

PHYTOPLANKTON LOSS THROUGH SINKING

Sinking Rate Determination

Four of the most pronounced epilimnial-hypolimnial biomass peaks were used as a measure of phytoplankton sinking rate. These peaks were May 13 to June 18, 1974 (36 days), July 29 to August 26, 1974 (28 days), and April 20 to May 31, 1973 (41 days) in the main reservoir; and April 27 to June 3, 1973 (37 days) in the Elk Creek Arm (Figures 5 and 6). The average peak interval was 35.5 days based on these four peak pairs. The depth of sinking was from the mid-epilimnion depth of 3 m to 30 m, a sinking depth of 27 m. Therefore, the average sinking rate was 0.76 m/day. Of course, sinking rate varies with water density, movements, viscosity, and size and shape of phytoplankton cells. The rate of 0.76 m/day is averaged over different seasons and is based on biomass peaks of the different algae found in Dworshak. Sinking rates measured in laboratory conditions range from 0.26 m/day for large, chain-forming algae to

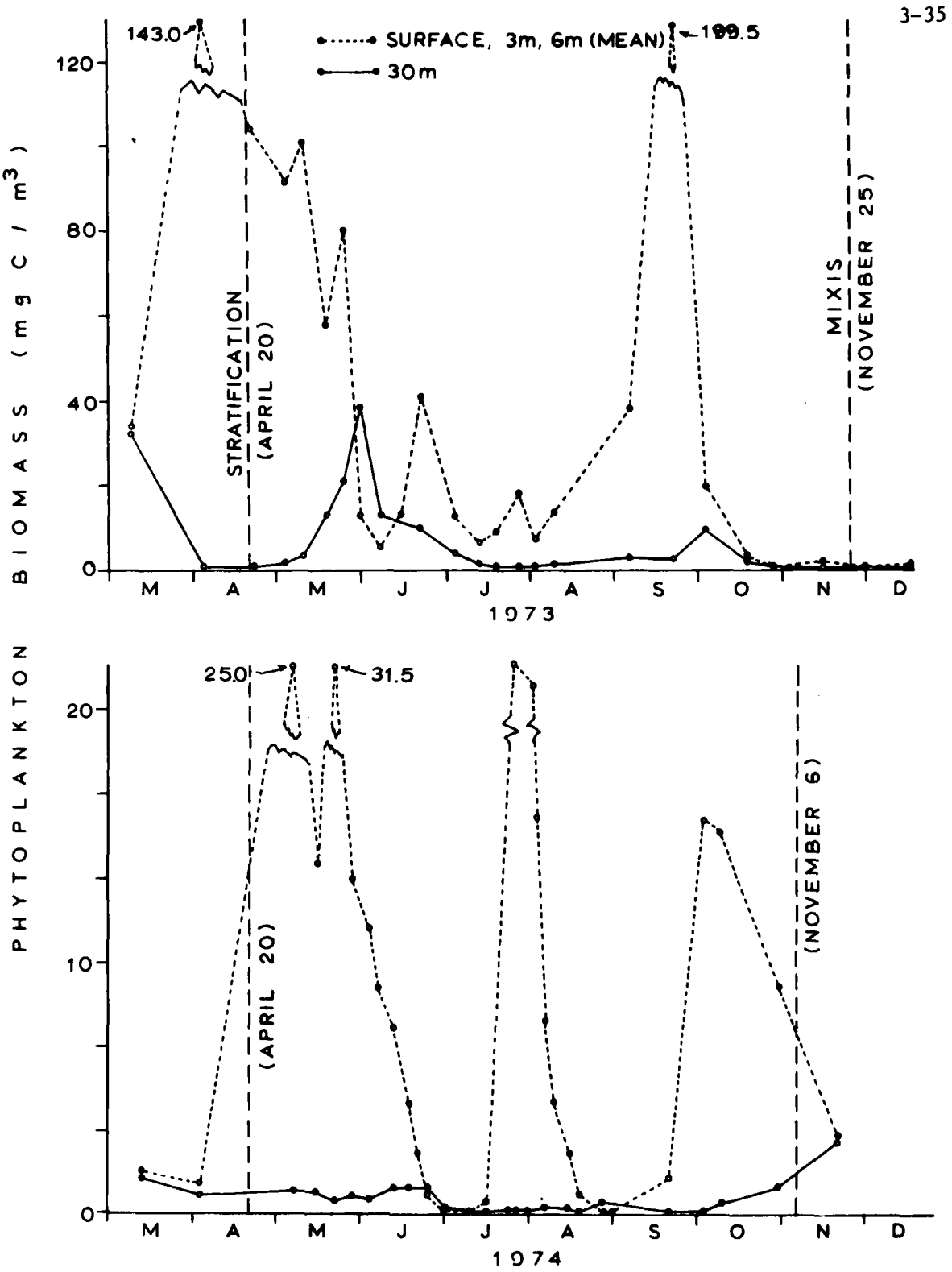


Figure 5. Average phytoplankton biomass in the epilimnion (surface, 3 m, 6 m) compared to biomass below the epilimnion (30 m) in Dworshak Reservoir (main reservoir station), 1973 and 1974.

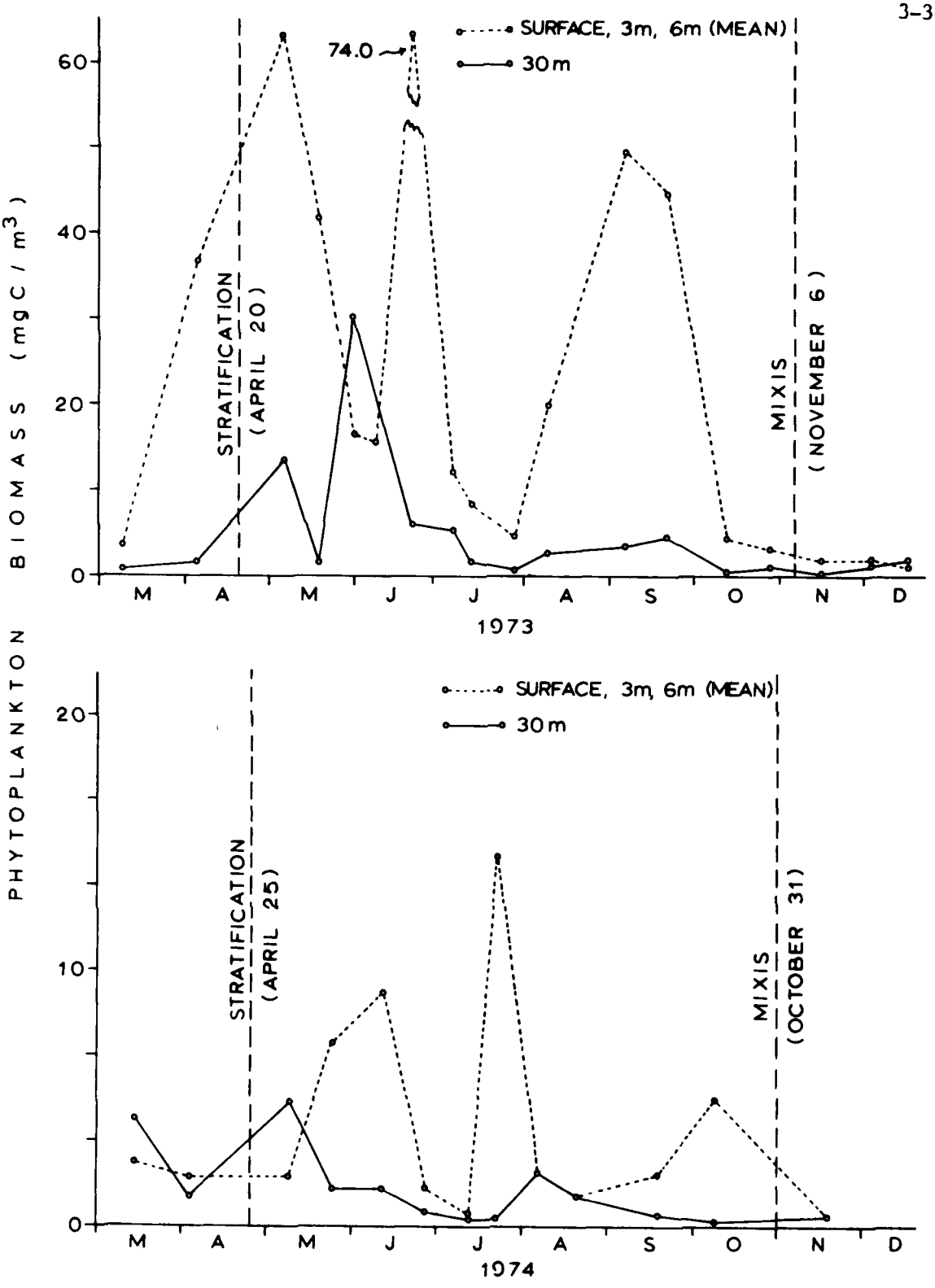


Figure 6. Average phytoplankton biomass in epilimnion (surface, 3 m, 6 m) compared to biomass below the epilimnion (30 m) in Dworshak Reservoir (Elk Creek Arm), 1973 and 1974.

1.95 m/day for the smallest centric forms and averaged 0.74 m/day (Smayda et al., 1966) which indicates that sinking rates calculated in Dworshak are reasonable.

Sinking Losses

Sinking losses to the hypolimnion were calculated by multiplying the hypolimnial phytoplankton biomass, during each sample period, by 0.76 m/day, the sinking rate. This is necessary since the concentration at 30 m is not the same as the sinking loss from the epilimnion. The sinking rate is less than one meter per day and the 30 m concentration must be multiplied by 0.76 m/day.

Phytoplankton losses due to sinking were similar between the main reservoir and the Elk Creek Arm during both years of the study. However, average annual losses were much higher in 1973 than in 1974. Actual phytoplankton loss to sinking averaged 4.9 mgC/m^3/day in 1973 and 0.4 mgC/m^3/day in 1973 and 0.9 mgC/m^3/day during 1974 in Elk Creek Arm (Tables 5, 6, and 7).

Phytoplankton at 30 m averaged 45.7% of the epilimnial biomass during stratification and 43.3% during mixis in the main reservoir in 1973. These percentages were 39.0% and 48.5 percent, respectively, in the Elk Creek Arm in 1973. This indicates that sinking losses to the hypolimnion occurred at approximately the same rate during mixis and during stratification in 1973. However, in 1974, the year when the reservoir was two to three times more turbid during the spring and early summer than in 1973, the average percentage of epilimnial biomass sinking during mixis was 2.3 times larger than during stratification in the main reservoir. The percentage was 2.0 times larger in the Elk Creek Arm in 1974 than in 1973

(Table 10). A larger percentage of phytoplankton sinks out of the epilimnion during mixis in a year of high turbidity than in a year of low turbidity. High turbidity throughout Dworshak in 1974 was due to spring runoff. The fine silt from surface erosion was carried in by tributaries and from within the reservoir where shorelines eroded and steep banks slid into the reservoir. It is probable that the high turbidity increased algal sinking rates through adsorption of silt particles to algal cells thereby increasing their density. This phenomenon has been documented in a study by Stanford et al. (1976) on Flathead Lake, Montana. Clay sediment flows into Flathead Lake annually in mid to late May and as turbidity settles through the water column clay-phytoplankton flocs form and sink. This process removes much of the algae, nutrients, and detritus from the upper layers and is considered by Stanford to be the single most important phenomenon limiting production in Flathead Lake.

PHYTOPLANKTON RECYCLED WITHIN THE EPILIMNION

The fraction of phytoplankton production which is not lost from the epilimnion through sinking or lost to the higher trophic levels through zooplankton grazing remains in the epilimnion. It is recycled through death of cells and their subsequent decomposition by bacteria and is again made available for uptake by phytoplankton cells.

Accurate methods to directly measure the recycling rate of phytoplankton communities have not been developed. However, an indirect measurement can be made if the total loss and the loss in other fractions is known. The recycled fraction in Dworshak was calculated for each sample period by subtracting the average loss to sinking and the average loss to

Table 10. Phytoplankton biomass at 30 m as a percentage of epilimnial phytoplankton biomass.

Station	Year	Percentage during mixis			Percentage during stratification	Average spring turbidity (FTU)
		Spring	Fall	Average		
Main Reservoir	1973	52.6	34.0	43.3	45.7	3.3
Main Reservoir	1974	70.7	97.4	79.6	34.6	6.7
Elk Creek Arm	1973	14.9	70.9	48.5	39.0	3.1
Elk Creek Arm	1974	116.0	182.3	138.1	69.4	11.9

grazing from the calculated average total loss of phytoplankton (Tables 5, 6, and 7).

The amount of phytoplankton recycled within the epilimnion was more than the total loss to grazing and sinking during 1973 and 1974 in both areas of the reservoir. Phytoplankton recycled amounted to an average of 89.5% of the total phytoplankton loss throughout the study (Tables 11 and 12) or an average of 124.42 $mgC/m^3/day$.

Bacterial Concentrations and Phytoplankton Recycling

Since phytoplankton carbon recycling is dependent upon bacterial activity, organic carbon levels should show some relationship to bacterial concentrations in the epilimnion. The total quantity of phytoplankton carbon recycled in 1973, averaged over both sections of the reservoir, was approximately 6 times more than in 1974. The average annual bacterial concentration, averaged over both sections of reservoir was 2.5 times higher in 1973 than in 1974 (Table 13).

More specific relationships as on a sample to sample basis are not obvious. Bacterial concentrations can increase through utilization of other carbon sources such as dead zooplankton, zooplankton carapaces, and zooplankton fecal material. Zooplankton are known to feed on bacteria and it is possible that bacterial concentrations could be decreased by zooplankton grazing (Nauwerck, 1963). Also, bacterial numbers do not, accurately, reflect the dynamics of the bacterial population since turnover is very rapid.

Table 11. Monthly and annual epilimnial phytoplankton carbon budgets for 1973 and 1974 in Dworshak Reservoir (main reservoir station).

	Depth of epilimnion (m)	Net phytoplankton production (mg C/m^2)	Phytoplankton biomass change (mg C/m^2)	Phytoplankton loss through grazing (mg C/m^2)	Phytoplankton loss through sinking (mg C/m^2)	Phytoplankton recycled within epilimnion (mg C/m^2)
1973						
April	0.6	479.4	+61.6	387.6	30.2	0
May	6.7	16,373.0	-18,030.2	23,430.8	2,226.7	8,745.7
June	7.6	27,886.9	+3,918.9	6,458.9	2,565.8	14,943.3
July	7.6	20,288.7	-3,173.3	2,777.1	447.3	20,237.6
August	10.1	104,235.4	+4,017.1	3,059.4	310.8	95,848.1
September	12.8	167,608.8	+32,057.1	36,687.4	1,137.1	97,727.2
October	16.8	62,648.8	-56,286.0	13,955.3	1,465.8	103,513.7
November	6.1	16,513.4	+13.4	213.0	47.4	16,239.6
Total		416,034.4	-37,421.4	87,969.5	8,231.1	357,255.2
Percent of total loss				19.4	1.8	78.8
1974						
April	3.1	1,364.4	+361.0	18.6	22.3	962.6
May	4.6	11,346.8	-109.5	91.1	77.3	11,287.9
June	6.1	17,361.3	-2,164.1	250.3	124.7	19,150.4
July	5.5	19,156.7	3,497.6	3,632.9	22.7	12,003.5
August	7.6	12,582.9	-690.0	2,836.9	39.5	10,385.5
September	10.7	31,757.9	2,492.9	897.7	34.2	28,333.1
October	13.7	34,313.7	-64.4	1,714.1	263.5	32,400.5
November	6.1	5,927.3	-220.8	55.1	58.9	6,034.1
Total		133,811.0	+3,113.7	9,496.7	643.1	120,557.6
Percent of total loss				7.3	0.5	92.2

Table 12. Monthly and annual epilimnial phytoplankton carbon budgets for 1973 and 1974 in Dworshak Reservoir (Elk Creek station).

	Depth of epilimnion (m)	Net phytoplankton production (mg C/m^2)	Phytoplankton biomass change (mg C/m^2)	Phytoplankton loss through grazing (mg C/m^2)	Phytoplankton loss through sinking (mg C/m^2)	Phytoplankton recycled within epilimnion (mg C/m^2)
1973						
April	2.4	2,769.8	+711.4	48.8	79.8	1,929.8
May	6.1	20,280.6	-3,930.4	13,283.6	1,485.3	9,442.1
June	7.6	36,727.2	+3,158.7	22,213.6	2,564.0	8,790.9
July	7.0	33,032.2	-6,675.3	6,713.2	510.0	32,484.3
August	8.8	452,779.7	+6,121.6	2,550.7	511.4	443,596.0
September	12.2	308,757.3	-3,725.5	9,249.9	909.1	302,323.8
October	15.3	184,718.3	-10,421.8	3,231.4	117.9	191,790.8
November	3.1	6,315.3	-11.8	15.4	9.0	6,302.7
Total		1,045,380.4	-14,773.1	57,306.6	6,186.5	996,660.4
Percent of total loss				5.4	0.6	94.0
1974						
April	1.5	125.0	-2.2	0.5	16.5	110.2
May	3.1	4,808.4	+600.4	25.0	186.6	3,996.4
June	4.6	17,447.5	-993.0	186.6	105.7	18,148.2
July	6.1	72,647.1	+1,353.6	3,029.7	96.9	68,166.9
August	9.1	3,673.9	-1,903.6	2,826.8	308.1	2,442.6
September	13.7	11,350.1	+808.0	774.1	172.6	9,595.4
October	10.7	10,926.6	-309.8	410.3	72.1	10,754.0
November	0					
Total		120,978.6	-446.6	7,253.0	958.5	113,213.7
Percent of total loss				6.0	0.8	93.2

Table 13. Comparison of annual quantities of phytoplankton carbon recycled within the epilimnion with average annual epilimnial total bacteria concentrations in Dworshak Reservoir during 1973 and 1974.

Station	1973		1974	
	Carbon recycled (mgC/m^2)	Total bacteria (#/ml)	Carbon recycled (mgC/m^2)	Total bacteria (#/ml)
Main Reservoir	357,255	48,653	120,558	14,231
Elk Creek Arm	996,660	48,035	113,213	29,004

PRIMARY PRODUCTION EFFICIENCY

The ratio of primary production to total chlorophyll may be an indicator of whether losses of phytoplankton are due to cell removal (grazing or sinking) or due to a limiting factor such as nutrients, light, temperature, etc. A decline in the production:chlorophyll ratio should indicate that the biomass loss is due to decreased efficiency of production and not removal of cells. Conversely, a high or increasing production:chlorophyll ratio which coincides with a loss of phytoplankton indicates that the loss is due to cell removal.

Cell removal through sinking was relatively constant and low during 1974 in the main reservoir. Cell removal through grazing reached three peaks; one during mid June, one in late July, and one in late October (Table 6 and Figure 3). These three peaks, which made up only a part of the total loss during those periods coincide with high production:chlorophyll peaks (high efficiency peaks). Losses which peak in mid-May, mid-July, and mid-September coincide with low photosynthetic efficiency peaks and indicate that loss is due to algal die-off rather than removal through grazing (Figure 7). Grazing, sinking, and die-off are,

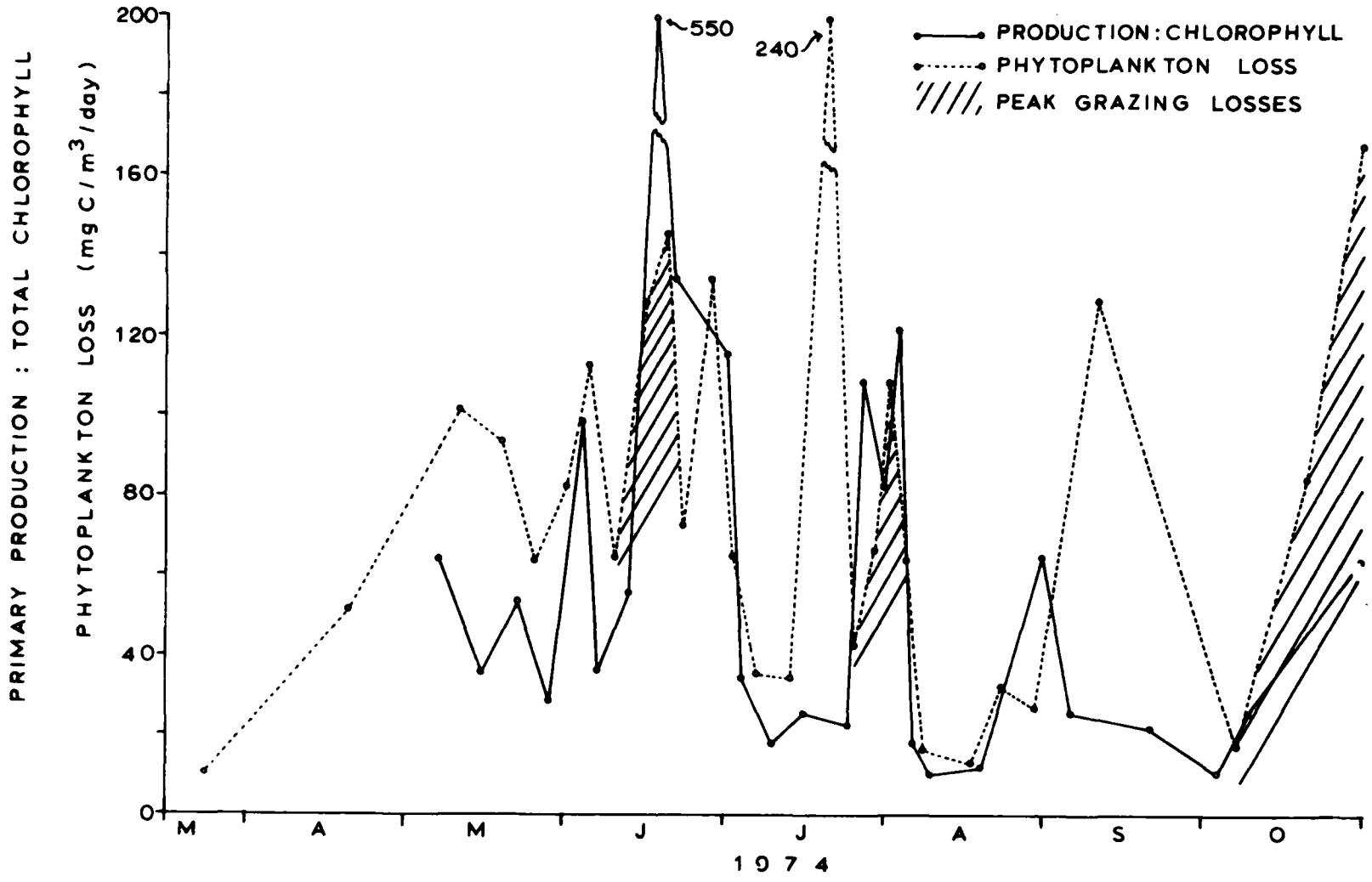


Figure 7. Primary production to total chlorphyll ratio compared to total phytoplankton loss as an indicator of production efficiency in Dworshak Reservoir (main reservoir station), 1974.

of course, occurring at all times and no one factor alone is responsible for a high loss rate.

EPILIMNIAL CARBON BUDGET

Phytoplankton carbon lost through grazing, sinking, recycling, and biomass gains or losses were calculated as $mgC/m^2/day$ by multiplying volumetric data (Tables 5, 6, and 7) by the depth of the epilimnion at the time of sampling. These were averaged monthly and multiplied by the number of days in each month when the reservoir was stratified. The result is a monthly and annual epilimnial phytoplankton carbon budget based on changes within a m^2 column of water extending from the surface to the bottom of the epilimnion. The totals of these losses and biomass changes is net phytoplankton production for each month and year (Tables 11 and 12).

The annual percentages (March-December) of phytoplankton grazed, lost to the hypolimnion, and recycled within the epilimnion were calculated for each station. These percentages or ratios were similar throughout both years and stations. Grazing losses during 1973 in the main reservoir were, however, two to three times larger than in other years and stations, a result of high zooplankton numbers during the spring diatom pulse. Carbon loss percentages averaged for 1973 and 1974 over both sections of reservoir were 9.5% loss to grazing, 0.9% loss to sinking, and 89.5% recycled within the epilimnion. In Canyon Ferry Reservoir during September and October, 1956, Wright (1958) found that 25.8% of production was lost to the hypolimnion and 72.6% was grazed. The remainder, 1.6%, was a gain in phytoplankton biomass over the two months. Total loss estimates were calculated on the basis of production minus biomass;

sinking loss estimates were based on concentrations of phytoplankton in the hypolimnion; gain in phytoplankton biomass was the net increase in biomass from beginning to end of study; and grazing loss estimates were the remainder of total loss. Wright disregarded recycling in his phytoplankton loss budget.

ZOOPLANKTON POPULATION DYNAMICS

Grazer Production

Accurate calculation of net zooplankton production requires information of the weight increment of individuals during their life span from hatching until death. Assumptions that must be made are that the population have a constant rate of recruitment and that there is no mortality of eggs and juveniles. Also, cohorts must be sampled through their life span, a process complicated by overlapping cohorts. A simple but less accurate method to estimate average production ($\overline{P}_t$) over time (t) is to divide the average population biomass ($\overline{B}_t$) by the turnover rate of biomass ($\overline{T}_B$). Turnover rate of a given population biomass is defined as the period of time during which, as a result of reproduction, growth and elimination, a complete change of biomass takes place (Edmondson, 1971). An average turnover time can be estimated by averaging the time between biomass peaks and biomass lows. This method was used by Wright (1965) in estimating Daphnia spp. production and can only be used if sampling frequency is shorter than the turnover time.

The average turnover rate for Daphnia schodleri, based on the average time between biomass highs and lows (Table 14) in Dworshak during 1974, was 16.4 days; turnover rate for Bosmina longirostris was 13.9 days. D. schodleri and B. longirostris biomass values averaged 41.58 and 2.83

Table 14. Zooplankton biomass (mgC/m^3) averaged through a 1m, 10 m, and an oblique tow in Dworshak Reservoir during March-November, 1974 (main reservoir station).

Date	*Daphnia schodleri*	*Bosmina longirostris*	*Ceriodaphnia reticulata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Cyclops bicuspidatus thomasi*	Total zooplankton biomass
March 13	.431	.005	.001	0	0	.268	.705
April 4	.332	.002	0	0	0	.189	.523
May 4	5.575	2.093	.001	0	0	2.970	10.639
May 7	.242	.016	.004	0	0	1.779	2.041
May 14	.146	.003	.001	0	0	.444	.594
May 22	.068	.066	0	0	0	.457	.591
May 28	.484	.448	.033	0	.041	1.269	2.275
June 7	5.721	.552	.043	0	0	2.659	8.975
June 10	5.917	1.910	0	0	0	6.048	13.875
June 20	37.434	9.448	.082	.036	0	14.495	61.495
June 25	12.740	1.571	.357	.162	0	8.458	23.288
July 1	58.185	9.500	.834	.433	0	25.364	94.316
July 4	56.774	2.306	.339	1.201	1.374	6.535	68.529
July 19	146.171	8.580	.181	.301	1.281	18.844	175.358
July 16	111.007	.761	0	.322	.819	4.328	117.237
July 23	108.843	5.568	.023	.327	1.086	3.727	119.574
July 26	51.257	3.607	0	5.203	23.848	1.129	85.044
July 30	274.099	7.448	0	6.809	40.025	1.642	330.023
August 2	70.319	1.803	0	.961	7.623	.909	81.615
August 6	92.335	1.379	.027	3.735	.881	.685	99.042
August 19	88.143	14.157	.215	28.671	.811	1.040	133.037
August 27	40.757	1.151	.825	59.915	1.679	1.060	105.387
August 30	22.039	1.624	.679	118.887	1.096	.743	145.068
September 5	3.112	.277	6.786	86.907	1.064	.515	98.661
September 20	7.813	.995	18.596	7.136	0	1.896	36.436
October 3	2.081	4.639	13.305	11.807	0	4.565	36.397
October 8	1.847	1.787	14.288	1.524	0	1.961	21.407
October 29	.594	.022	3.619	1.663	0	16.026	21.924
November 19	1.320	.511	.707	.090	0	9.640	12.268

mgC/m^3, respectively, during 1974. The average production rate (March-November), based on turnover rates and biomass averages, was 2.53 $mgC/m^3/day$ for D. schodleri and 0.20 $mgC/m^3/day$ for B. longirostris or a total net production of 2.73 $mgC/m^3/day$. D. schodleri and B. longirostris were the predominant forms in 1974 comprising 73% of the total grazer biomass. Assuming that D. schodleri and B. longirostris production was representative of the remaining 27% biomass, expanding the production on the basis of biomass gives an average total grazer production rate of approximately 3.74 $mgC/m^3/day$.

Transfer Efficiency

The average net primary production in Dworshak Reservoir during 1974 (March-November) was 58.09 $mgC/m^3/day$ (Table 2). The ratio of primary net production to secondary net production or transfer efficiency was 15.5%. This appears to be a reasonable estimate since transfer efficiency between primary and secondary trophic levels usually lies between 10-20% (Odum, 1971).

Wright (1965) calculated a transfer efficiency of 13.5% in Canyon Ferry Reservoir for two species of Daphnia which were the predominant grazers. However, grazing losses in Canyon Ferry were 72.6% of the primary production compared to only 9.5% in Dworshak. This comparison indicates that zooplankton may be utilizing primary production in the form of dead algal cells, detritus, bacteria, and/or dissolved organic material. A large part of what we refer to as "phytoplankton recycled within the epilimnion" may be eaten by zooplankton.

Assimilation Efficiency

Assimilation is the conversion of digested food into structural materials of the animal. This term is often confused with absorption of ingested food. The average intake of phytoplankton by zooplankton (loss to grazing) was 7.85 mgC/m^3/day in Dworshak during 1974 (Table 6). Assuming an absorption efficiency of 85% (Blazka, 1971; Wright, 1965), 6.67 mgC/m^3/day were absorbed for utilization by grazers. Part of this absorbed carbon went to synthesis of zooplankton body structure and the remainder was used in respiration. Net zooplankton production, calculated previously, is an estimate of synthesis which can be subtracted from absorption to determine respiration. Absorption of 6.67 mgC/m^3/day minus synthesis of 3.74 mgC/m^3/day yields 2.93 mgC/m^3/day respiration or a grazer assimilation efficiency of 56%.

Zooplankton Birth Rates

It is probable that zooplankton production is directly affected by phytoplankton production. The dependence of zooplankton on phytoplankton as a food source is suggested by birth rates of the predominant zooplankton in Dworshak. Instantaneous rates of birth were calculated for D. schodleri and B. longirostris at the main reservoir station in 1974 (Table 15). Birth rates were not determined for other cladocerans because of their low numbers or for C. bicuspidatus thomasi because of difficulties with egg preservation and counting. Hall's (1964) method as applied to D. galeata mendota was used in the instantaneous birth rate calculation:

$$b = \ln (1 + B)$$

where b is the instantaneous birth rate and B, the finite birth rate, is given by:

Table 15. Calculation of *Daphnia schodleri* and *Bosmina longirostris* instantaneous birth rates (b) in Dworshak Reservoir (main reservoir station), 1974.

		D. schodleri					*B. longirostris*				
1974	Average epilimnial water temperature (°C)	Adults/m^3	Eggs/m^3	Egg duration* (days)	Finite birth rate (B)	Instantaneous birth rate (b)	Adults/m^3	Eggs/m^3	Egg duration* (days)	Finite birth rate (B)	Instantaneous birth rate (b)
March 13	3.3	69.5	9.3	16+	.008	.008	2.6	0	15+	0	0
April 4	3.8	53.6	9.1	16+	.011	010	1.3	0	15+	0	0
May 4	7.1	899.2	1,881.1	16+	.139	.130	1,162.9	337.4	15+	.019	.018
May 7	10.3	39.1	–	8.3	–	–	9.1	1.7	14.6	.013	.012
May 14	11.3	23.5	43.3	6.8	.271	.239	1.9	3.0	8.5	.186	.170
May 22	12.2	11.0	41.5	6.2	.609	.476	36.9	14.9	7.3	.055	.053
June 7	13.7	922.7	202.9	4.8	.046	.043	306.9	19.6	6.0	.011	.010
June 10	14.0	954.3	458.9	4.6	.105	.095	1,061.3	68.8	5.7	.011	.011
June 20	14.3	6,037.7	3,638.8	4.3	.140	.130	5,248.8	1,933.4	5.5	.067	.064
June 25	14.4	2,054.8	323.3	4.3	.037	.034	872.7	126.8	5.5	026	.025
July 4	14.8	9,157.1	2,482.9	4.1	.066	.063	1,281.3	169.3	5.2	.025	.024
July 9	14.9	23,576.0	2,303.8	4.1	.024	.023	4,766.7	456.9	5.1	.019	.018
July 16	16.4	17,904.4	347.7	3.4	.006	.005	423.0	54.9	4.2	.031	.029
July 23	17.4	17,555.4	983.7	3.1	.018	.017	3,093.4	511.9	3.8	.043	.041
July 26	17.9	8,267.2	2,619.6	3.0	.106	.105	2,003.9	331.2	3.6	.046	.044
July 30	18.5	44,209.5	5,429.2	2.9	.042	.040	4,137.6	470.6	3.4	.033	.032
August 2	19.0	11,341.8	1,133.3	2.8	.036	.034	1,001.8	153.0	3.2	.048	.045
August 6	19.9	14,892.7	142.7	2.7	.003	.003	765.9	84.1	2.9	.038	.036
August 19	20.2	14,216.6	1,531.9	2.6	.041	.039	7,865.3	1,534.7	2.8	.070	.066
August 27	20.4	6,573.7	1,000.7	2.6	.059	.056	639.3	66.0	2.8	.037	.035
August 30	20.5	3,554.7	193.6	2.5	.022	.020	902.1	109.5	2.8	.043	.041
September 5	18.5	501.9	12.8	2.9	.009	.008	153.7	12.8	3.4	.025	.023
September 20	16.5	1,260.2	14.7	3.4	.003	.003	552.8	7.4	4.1	.003	.003
October 3	14.6	335.7	–	4.2	–	–	2,577.5	304.1	5.3	.022	.021
October 8	14.4	297.9	14.3	4.3	.011	.011	993.1	–	5.5	–	–
October 29	12.1	95.8	8.7	6.6	.014	.013	12.1	5.5	7.5	.061	.058
November 19	9.7	212.9	34.8	9.6	.017	.016	284.0	124.1	14.0	.031	.030

* Egg duration/temperature relationships from Kwik, J. K. and J. C. H. Carter (1975).

$$B = \frac{Ne}{DN}$$

in which N_e and N are the number of embryos and the number of animals, respectively, and D is the embryonic development time at the respective water temperature. Egg development time for a range of temperatures has been determined for Daphnia sp. and Bosmina sp. by Kwik et al. (1975). Their estimates were used here to determine egg development times from known epilimnial water temperatures in Dworshak (Figure 8).

Birth rates for D. schodleri and B. longirostris followed similar trends in Dworshak. The average birth rate of D. schodleri was 0.065 and that of B. longirostris, 0.038 (Table 15). Birth rates for these two genera were estimated at 0.19 and 0.11, respectively, in a study by Kwik and Carter (1974). Wright (1965) estimated birth rates for Daphnia schodleri in Canyon Ferry Reservoir at 0.15 which is more than twice as high as rates in Dworshak. An explanation for this may be that Daphnia production in Canyon Ferry averaged 150 $mgC/m^2/day$ as comapred to only 2.53 $mgC/m^3/day$ in Dworshak Reservoir.

Grazing Selectivity

Zooplankton birth rates and phytoplankton standing crop appear to be related (Figure 9). Birth rates of both D. schodleri and B. longirostris increased with the spring diatom and green algae (Melosira and Mougeotia) pulses in 1974. With the May decrease in phytoplankton, birth rates of both genera decreased. Rates increased briefly following small diatom (Melosira) pulses in June and then dropped to a low in July. Birth rates increased again in late July, apparently, in response to a small-celled dinoflagellate (Dinobryon) which pulsed in late July. Both

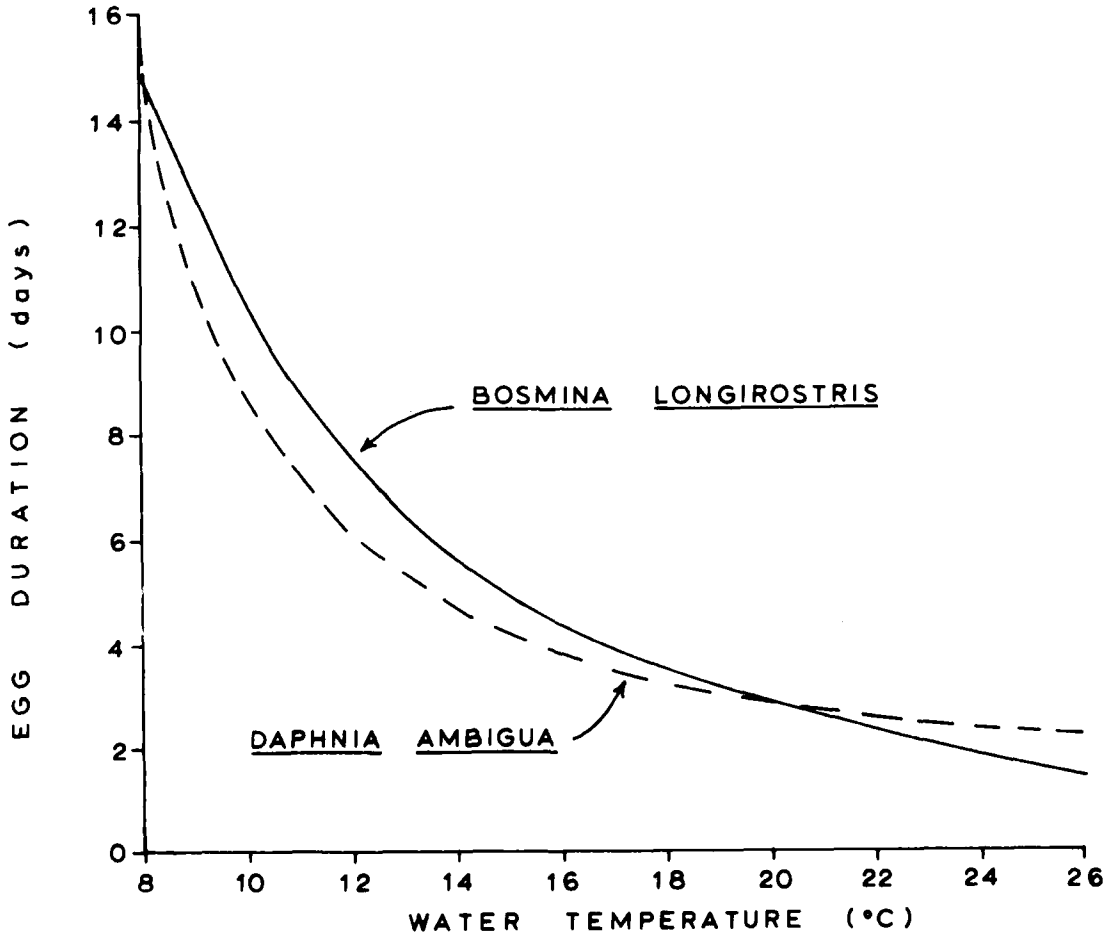


Figure 8. Duration of embryonic development in Daphnia ambigua and Bosmina longirostris at different water temperatures (from Kwik, J.K. and J.C.H. Carter, 1975).

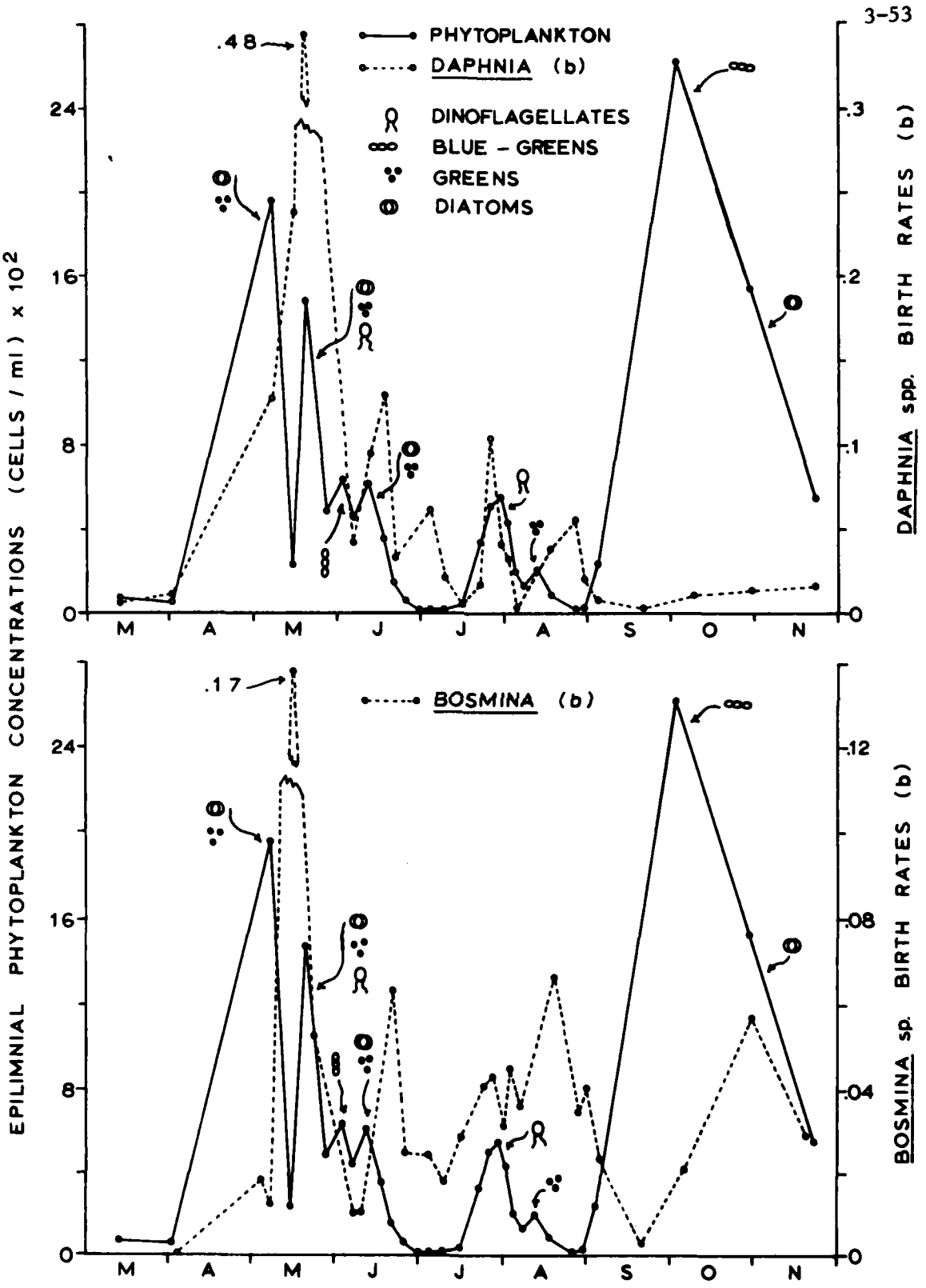


Figure 9. Epilimnial phytoplankton concentrations and composition related to Daphnia schodleri and Bosmina longirostris instantaneous birth rates (b) in Dworshak Reservoir (main reservoir station), 1974.

genera of cladocerans responded to the mid August peak of greens (Ankistrodesmus) with increased birth rates. Birth rates of D. schodleri remained low during the fall and into the winter. The predominant algal form during September and October was blue-green (Anabaena and Aphanizomenon), but D. schodleri birth rates did not respond to the very high concentrations (approximately 2.5 million cells/l) of blue-greens at that time. B. longirostris birth rates did rise during October but it is only speculative as to whether they responded to blue-greens or to a small pulse of diatoms (Melosira) in late October. A small, early pulse of blue-greens (Anabaena) did did not trigger an apparent birth rate response from either genus of grazer. Birth rate to phytoplankton biomass correlation coefficients through 1974 were r = .13 for B. longirostris and r = .59 for D. schodleri.

Selectivity studies indicate that filamentous blue-greens are rejected by cladocerans, especially Daphnia (Burns, 1966). Burns observed that Daphnia rosea also rejected single cells of Anabaena. Though quantitative evidence for selection is not abundant there is evidence that Daphnia does not select from mixtures of "desirable" algae as different in size and shape as Scenedesmus and Chlorella (Ryther, 1954). Birth rate responses of cladocerans to different algal forms in Dworshak Reservoir concur with the inferences drawn from phytoplankton biomass and grazing loss in a previous section on grazing losses (page 30) and it is concluded that D. schodleri and B. longirostris do not utilize blue-green algae in any significant amount but do utilize diatoms, greens, and small dinoflagellates in Dworshak Reservoir.

CONCLUSIONS

1. Primary Production and Algal Biomass:

   a) Primary production and algal biomass averaged 102.95 $mgC/m^3/day$ and 18.91 mgC/m^3, respectively, from March, 1973, through November, 1974 in Dworshak Reservoir.

   b) Annual average biomass was about twice as concentrated in the main reservoir as compared to concentrations in the Elk Creek Arm.

   c) Primary production was higher in 1973 than in 1974, partially due to high turbidity during the spring of 1974.

   d) The phytoplankton production rate averaged 5.5 times the algal biomass.

2. Algal Loss to Zooplankton Grazing:

   a) The average grazing coefficient for the entire grazing community was 0.01429 m^3/mg zooplankton C/day.

   b) The loss of phytoplankton from the epilimnion to zooplankton grazing averaged 24.67 $mgC/m^3/day$ or 9.5% of the total phytoplankton loss.

   c) Phytoplankton loss to grazing was reduced during seasons of high turbidity.

   d) Zooplankton did not, significantly, reduce the standing crop of phytoplankton.

   e) The correlation between grazer biomass and phytoplankton loss was low, $r = 0.03$.

3. Algal Loss to Sinking:

   a) Phytoplankton loss from the epilimnion through sinking averaged 3.98 $mgC/m^3/day$ or 0.9% of the total phytoplankton loss.

   b) The average phytoplankton sinking rate was 0.76 m/day.

4. Algal Loss to Recycling:

   a) An average of 89.6% of the phytoplankton production remained in the epilimnion and was recycled through death and bacterial decomposition.

   b) Total bacteria concentrations were largest in 1973 when phytoplankton recycling was six times greater than in 1974.

   c) Production:chlorophyll ratios indicated that algal biomass decreases were principally due to decreased production efficiency leading to increased die-off, not due to increased grazing.

5. Zooplankton Dynamics

   a) Average grazer production in 1974 was 3.74 $mgC/m^3/day$.

   b) Energy transfer efficiency from phytoplankton to zooplankton was estimated to be 15.5%.

   c) Grazer assimilation efficiency was 56%.

   d) Instantaneous birth rates for Daphnia schodleri and Bosmina longirostris averaged 0.065 and 0.038, respectively.

   e) Birth rates of both D. schodleri and B. longirostris increased during pulses of diatoms, small-celled dinoflagellates, and green algae; but D. schodleri birth rates did not respond to pulses of blue-green algae.

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BACTERIOLOGY

Part 4 of

EARLY LIMNOLOGY OF DWORSHAK RESERVOIR

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TABLE OF CONTENTS

Page

LIST OF TABLES 4-iii

LIST OF FIGURES 4-iv

INTRODUCTION 4-1

METHODOLOGY 4-2

- Sample Collection and Storage 4-2
- Total Bacteria Counts 4-2
- Total and Fecal Coliform Counts 4-2
- Soluble Carbon Concentrations 4-2
- Algal Assays 4-3
- Statistical Analysis 4-3
- Survival of Indicator Organisms in Dworshak Water 4-3

RESULTS AND DISCUSSION 4-5

- Total Bacteria 4-5
- Total and Fecal Coliforms 4-8
- Soluble Carbon 4-11
- Algal Assays 4-12
- Survival of Indicator Organisms in Dworshak Water 4-48
- Relationship of Total Bacteria, Soluble Carbon, and Total Coliforms to Other Parameters 4-55

CONCLUSIONS 4-62

LITERATURE CITED 4-63

LIST OF TABLES

Table Page

1. Simple correlations 4-58

LIST OF FIGURES

Figure		Page
1a.	Yearly means and ranges of the total bacterial count at RM-3, RM-19, RM-35, and EC-4 for the three sampling years	4-6
1b.	Top: yearly means and range of total bacterial count at LNFL-1 for the three sampling years; bottom: mean monthly count of total bacteria at RM-3 for the three sampling years	4-7
2a.	Yearly means of total coliform counts at RM-3, RM-19, RM-35, and EC-4 for the three sampling years	4-9
2b.	Top: yearly means of the total coliform count at LNFK-1 for the three sampling years; bottom: monthly mean surface count of total coliforms at RM-3 during the three sampling years	4-10
3.	Mean soluble carbon levels at RM-3, RM-19, RM-35, EC-4, and LNFK-1 during the three sampling years	4-13
4.	Monthly mean soluble carbon levels at RM-3	4-15
5.	Mean dry weight and nutrient stimulation comparisons of growth in RM-3 algal assays	4-16
6.	Mean dry weight and nutrient stimulation comparisons of growth in RM-19 algal assays	4-17
7.	Mean dry weight and nutrient stimulation comparisons of growth in EC-4 algal assays	4-18
8.	Mean dry weight and nutrient stimulation comparisons of growth in RM-35 algal assays	4-19
9.	Mean dry weight and nutrient stimulation comparisons of growth in LNFK-1 algal assays	4-20
10.	The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in October 1974	4-22
11.	The effect of phosphorus and nitrogen additon on growth of Selenastrum capricornutum in water from RM-3 in March 1975	4-23

Figure | Page

12. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in April 1975 4-24

13. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in May 1975 4-25

14. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in July 1975 4-26

15. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in October 1974 4-27

16. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in March 1975 4-28

17. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in April 1975 4-29

18. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in May 1975 4-30

19. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in July 1975 4-31

20. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in October 1974 4-32

21. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in March 1975 4-33

22. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in April 1975 4-34

23. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in May 1975 4-35

Figure | Page

24. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in July 1975 4-36

25. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in October 1974 4-38

26. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in April 1975 4-39

27. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in May 1975 4-40

28. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in July 1975 4-41

29. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in October 1974 4-42

30. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in April 1975 4-43

31. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in May 1975 4-44

32. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in July 1975 4-45

33. Survival rates of selected indicator organisms in filtered and unfiltered Dworshak water, 20 July 1973 . . 4-50

34. Survival of Escherichia coli, Streptococcus faecalis var. liquefaciens, Enterobacter aerogenes, and a Salmonella sp. in filtered Dworshak water, 3 August 1973 4-52

35, Survival of Escherichia coli, Streptococcus faecalis var. liquefaciens, Enterobacter aerogenes, and a Salmonella sp. in unfiltered Dworshak water, 3 August 1973 4-53

INTRODUCTION

Impoundment of the North Fork of the Clearwater River by Dworshak Dam created a new reservoir with great potential for recreation and other uses. The bacterial water quality as it relates to public health and the effects of bacterial activity as related to limnological parameters are important considerations in assessment of overall water quality in the reservoir.

The significance of bacteria as indicators of water quality deterioration from human or other animal input is obvious. More important, perhaps, in a new reservoir is the establishment of baseline levels of these organisms, thereby permitting determination of future water quality. In addition, if enough organic carbon enters the reservoir, either from allocthonous sources such as vegetation in runoff or autochthonous sources such as primary productivity, heterotrophic bacterial activity can deplete dissolved O_2, increase CO_2 levels, change pH, and produce toxic metabolites such as hydrogen sulfide with significant effects on the biota in the reservoir. Quality of the receiving body below the dam may also be lowered. The recycling of nutrients is also primarily a bacterial function and is consequently an important limnological consideration.

The objectives of this portion of the study were: (1) to assess the bacterial water quality from the public health viewpoint, (2) to evaluate the impact of bacterial activity on the limnological apsects of the reservoir, and (3) to project future direction of the bacterial population and its effect on reservoir water quality.

METHODOLOGY

Sample Collection and Storage: Bacterial samples were taken by Kemmerer bottle at the same sites and depths as other parameters in this study. Immediately after collection samples were cooled and transported from the site to the laboratory for analysis. Collection to analysis time was normally less than 24 hr but at times was as long as 48 hr due to distance, collection problems, etc.

Total Bacteria Counts: Total counts were made on nutrient agar (Difco Laboratories, Detroit, Michigan) by the pour plate technique. Appropriate dilutions of the sample in 0.1% tryptone were added to petri dishes to give plates containing between 30 and 300 colonies. Duplicate sets of plates were incubated at 25°C for one week and then counted with the aid of a Quebec colony counter. Although this counting technique has limitations, it was felt that the method did monitor a consistent population (that group of heterotrophic organisms which would grow on nutrient agar) throughout the study.

Total and Fecal Coliform Counts: Total and fecal coliforms were enumerated utilizing the membrane filter technique outlined in Standard Methods (1).

Soluble Carbon Concentrations: Soluble carbon concentrations were determined by combustion of readily oxidizable carbon with persulfate, a modification of the method of Burgess et al. (2). In this procedure

readily oxidizable carbon was converted to carbon dioxide (CO_2) and trapped in 2N sodium hydroxide (NaOH). The carbonate formed was then titrated with 1/12 N sulfuric acid (H_2SO_4) using a standard double titration procedure. Titration values were expressed in mg carbon as CO_2 per liter of water. The carbon detected in this procedure is referred to in this report as soluble carbon.

Algal Assays: Algal assays were conducted on samples from all sites during October 1974; April, May, and July in 1975; and from RM-3, RM-19, and EC-4 during March 1975 to determine limiting nutrients and algal growth potential of Dworshak water. Assays were conducted according to Algal Assay Procedure (3).

Statistical Analysis: The data were analyzed to determine simple correlations and regression coefficients among bacteria and various parameters by the Statistical Analysis System (SAS) (4). Algal assays were evaluated as means, standard deviations, and variances according to Statistical Methods (5) and the SAS. An F-test was used to determine significant differences between comparisons of treatments. The Harvey procedure (4) for calculating analysis of variance for data of unequal subclasses was also used in the analysis.

Survival of Indicator Organisms in Dworshak Water: Experiments were conducted to determine indicator organism survival using membrane chambers similar to those of McFeters and Stuart (6). Membrane chambers were constructed from 2-inch polyvinyl chloride tubing with

millipore filters fitted to both ends. A serum cap was fitted to the chamber for introduction of organisms and removal of samples. The filter chambers were filled with either filtered or non-filtered Dworshak water and a known number of indicator organisms. The chambers were then submerged 10 ft below the surface. Samples were withdrawn aseptically with sterile syringes and diluted after appropriate enrichment. The organisms and enrichments used were as follows: Escherichia coli, Enterobacter aerogenes and Salmonella; brain heart infusion (BHI) broth; Streptococcus faecalis var. liquefaciens, APT broth (all purpose medium with Tween 80). Samples were returned to the laboratory and plated after 2 hr enrichment time on appropriate selective media. E. coli and E. aerogenes were plated on Eosin Methylene blue agar, S. faecalis on KF Streptococcus agar, and Salmonella on brilliant green lactose bile agar. Plates were counted after 24 hr incubation at 37°C.

RESULTS AND DISCUSSION

Total Bacteria: Mean total bacterial concentrations in Dworshal pool during the sampling period were high (Fig. 1a, 1b-top). The highest mean surface count was at RM-19 during 1972 while the lowest mean count was at RM-3 during 1972. The highest mean deep level count was at LNFK-1 in 1973 and the lowest was at RM-3 in 1972. Highest mean counts for combined sample sites were recorded in 1973. Typical mean monthly fluctuations are seen in Fig. 1b-bottom. Bacterial numbers reached maximums in July 1972, May 1973, and July 1974. In 1973 the peak duration extended from May until September. In 1974 the peak duration extended only through June and July. Total bacterial production was consequently much greater in 1973 than in either 1972 or 1974. The maxima in 1973 corresponded to the times of decreased dissolved oxygen and the presence of hydrogen sulfide in the bottom waters.

The range of bacterial numbers was broad (Fig. 1a, 1b). The highest individual sample count recorded (1.6×10^6 bacteria/ml) was at LNFK in August 1973. Fortunately, counts of this magnitude were not common.

The high bacterial counts prevalent in the pool throughout the sampling period was undoubtedly due to high organic levels in the reservoir. The organic levels in the reservoir were due in part to leaching of sediment, submerged vegetation, and shoreline materials but also to the relatively high primary production. Often bacterial

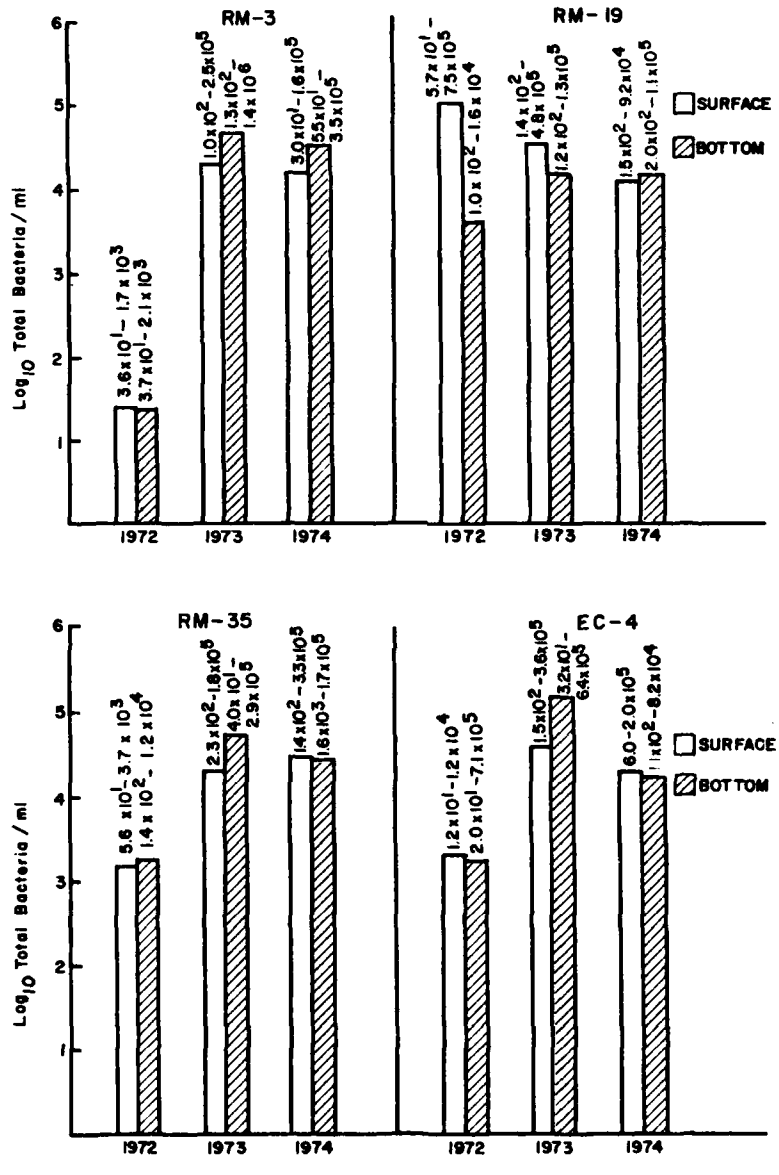


Figure 1a. Yearly means and ranges of the total bacterial count at RM-3, RM-19, RM-35, and EC-4 for the three sampling years

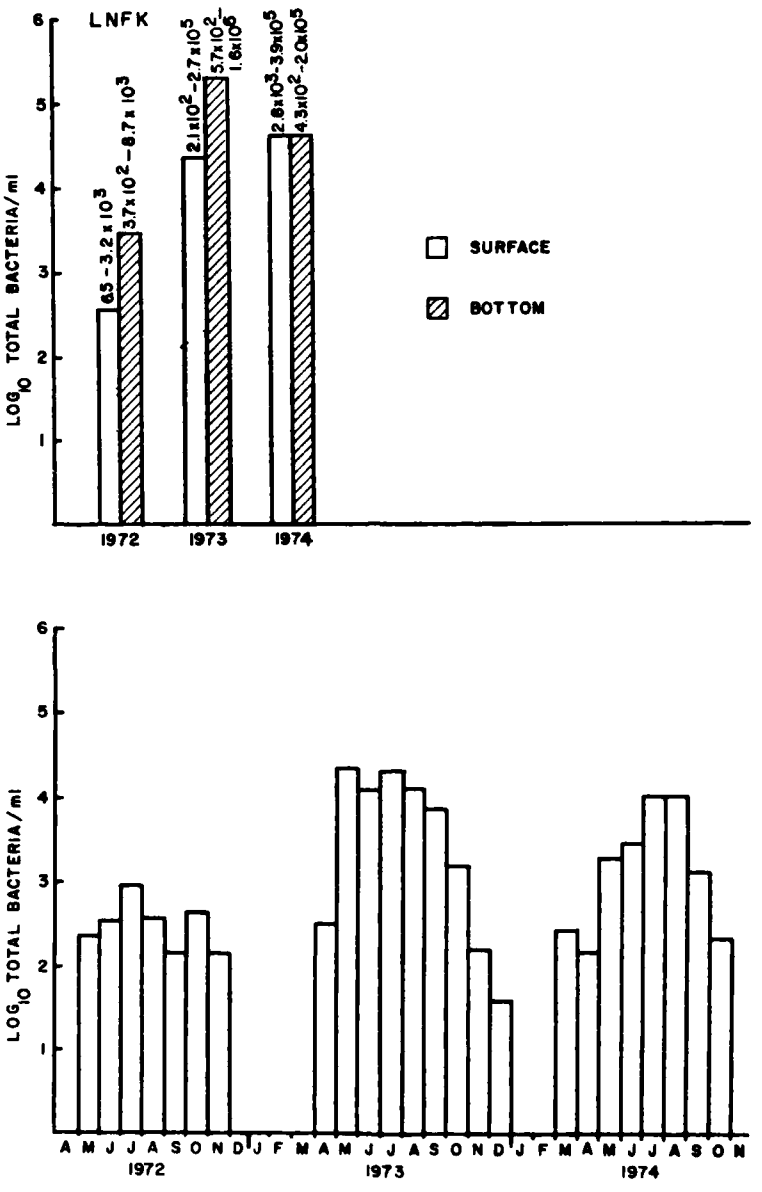


Figure 1b. Top: yearly means and range of total bacterial count at LNFK-1 for the three sampling years; bottom: mean monthly count of total bacteria at RM-3 for the three sampling years.

numbers fluctuated in the same pattern as algae numbers and were probably using exudates from photosynthetic activity as an energy source during initiation of productivity peaks. Bacterial levels were then maintained by breakdown of algal cells which accounted for the longevity of the bacterial peaks. Oxygen consumption by these bacterial activities was significant at times as indicated by low D.O. and anaerobic conditions, particularly during 1973.

Total and Fecal Coliforms: Coliform bacteria were always present in the reservoir during the sampling period. Mean total coliform counts followed the same general yearly pattern as did total bacterial counts with the exception of the EC-4 site (Fig. 2a, 2b-top). Instead of a maximum peak in 1973 and subsequent decline in 1974 as exhibited at the other sites, total coliforms progressively increased at the Elk Creek site throughout the three sampling years. It must be emphasized, however, that these coliforms do not appear to be related to any source of pollution but are in fact a part of the flora of the reservoir. Consequently, their numbers increase as do the total bacterial numbers during the summer months (Fig. 2b-bottom). Evidence for coliform growth rather than allochthonous input stems from the extremely high numbers observed in some cases and also from the general lack of fecal coliforms in the water system.

Fecal coliforms were found only at LNFK-1 in the fall of 1972. The level was 2 fecal coliforms/100 ml and presence was attributed to deer and elk migration or water fowl usage during that time. In 1973,

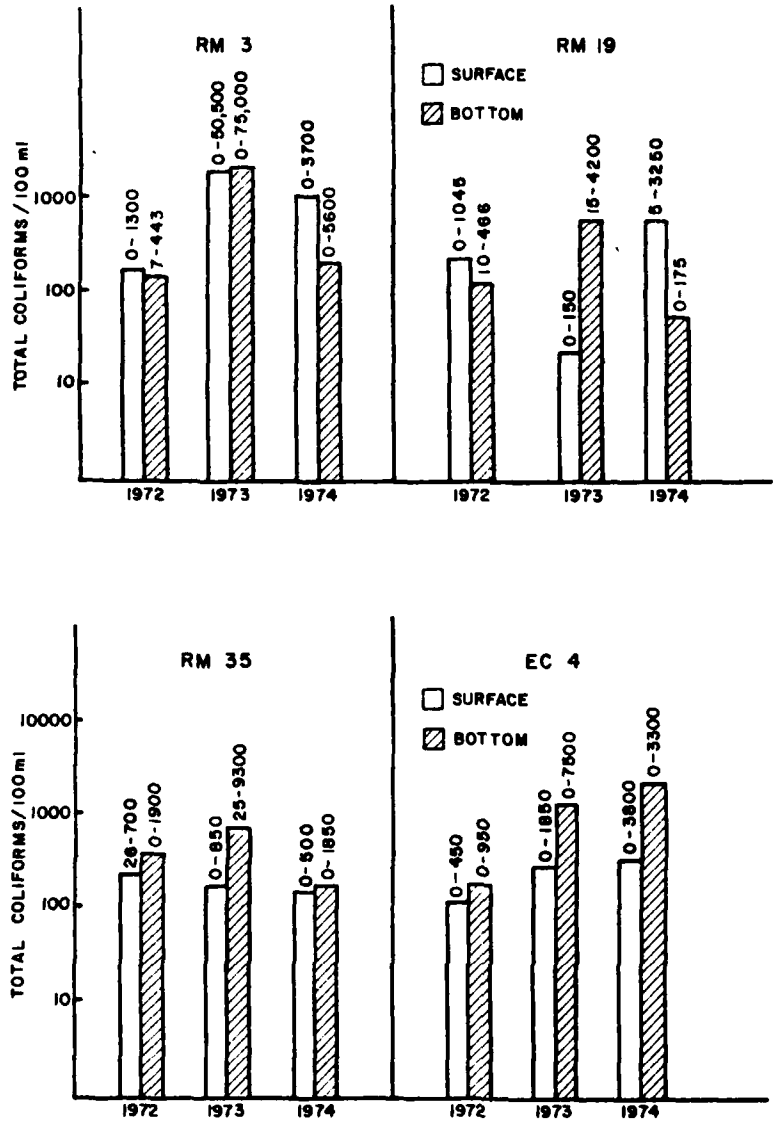


Figure 2a. Yearly means of total coliform counts at RM-3, RM-19, RM-35, and EC-4 for the three sampling years

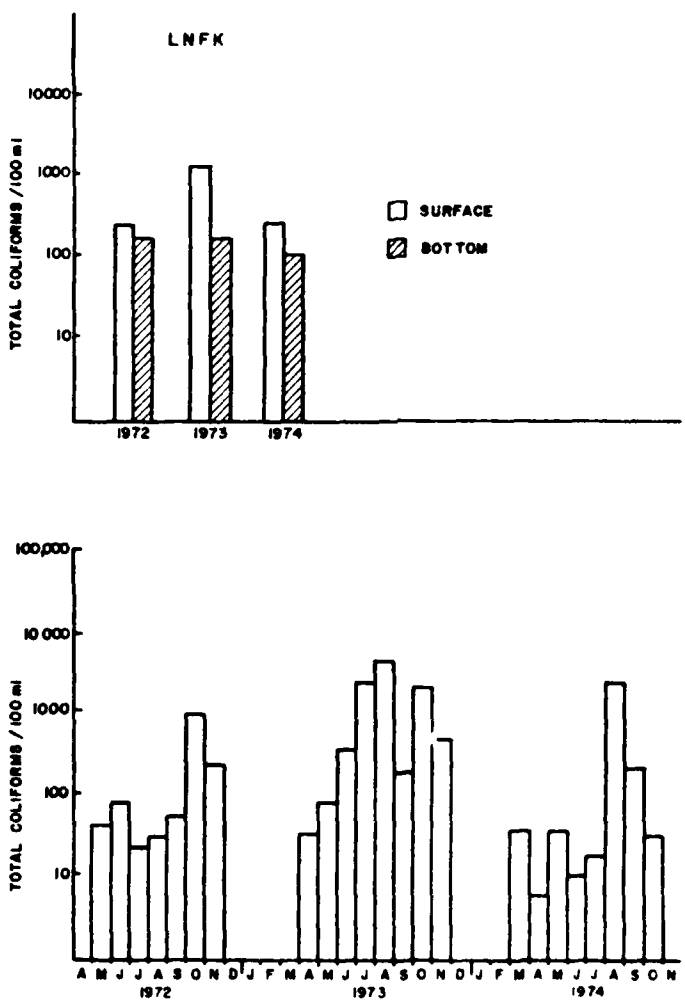


Figure 2b. Top: yearly means of the total coliform count at LNFK-1 for the three sampling years; bottom: monthly mean surface count of total coliforms at RM-3 during the three sampling years

fecal coliforms were detected again in the fall at LNFK and also at RM-35. Numbers were sporadic and reached a significant level (45 fecal coliforms/100 ml) only at RM-35 in November. In the spring of 1974 fecal coliforms were occasionally isolated from every sampling site. Numbers were always less than 5/100 ml. These coliforms were probably associated with runoff since no further fecal coliform isolations were made after July 1 of that year.

The continued increase in total coliforms at EC-4 in both the surface and deep samples may constitute a minor area of concern. It is possible that a portion of the coliforms arise from effluents from the town of Elk River or as a result of nutrient loading from disposal activities in the area. In any event, the high total coliform levels do not constitute a violation of the Idaho water quality standards (7). Total coliform standards in the Idaho standards are limited to use in waters where there are identifiable fecal sources, which is not the case in the Dworshak pool. With the exception of a minor potential problem at EC-4, it was not felt that the total coliform levels indicate any public health danger.

Soluble Carbon: Persulfate oxidizable carbon has been shown by Gilmour et al. (8) to be that carbon which is initially decomposed by bacteria in the BOD_5 procedure. In addition, they found that the initial fraction of the total carbon that was decomposed was a soluble carbon fraction.

In an aquatic sample, the fraction of carbon most usable and consequently the one most often cycled would be the soluble fraction.

Therefore, the soluble fraction largely dictates the growth of the heterotrophic bacterial population.

A large amount of soluble carbon should have been available early in the impoundment period of the reservoir due to vegetation, soil organic material, and timber leachate in the impoundment area. In subsequent years it would be expected that the soluble carbon levels would decrease due to losses during and after immobilization and mineralization of the carbon.

Reduction in soluble carbon levels as proposed was generally the pattern that was seen in Dworshak Reservoir (Fig. 3). Soluble carbon levels at RM-3, EC-4, and LNFK-1 decreased throughout the sampling period. Consequently, it is not expected that decreased dissolved oxygen or hydrogen sulfide production will be future problems in the reservoir unless massive primary production is experienced.

Soluble carbon at RM-35 and RM-19 increased in 1974. The increase at these sites could be due to increased primary productivity. There seems to be no good reason to expect the observed increases to continue, at least not to levels which would cause water quality problems.

Monthly averages of soluble carbon levels are shown in Fig. 4. Minimum carbon levels coincide with times of maximum bacterial numbers reinforcing the relationship between these two parameters.

Algal Assays: Mean dry weights for all experiments at each site are shown in Figs. 5-9. In every case the statistical analysis, i.e.,

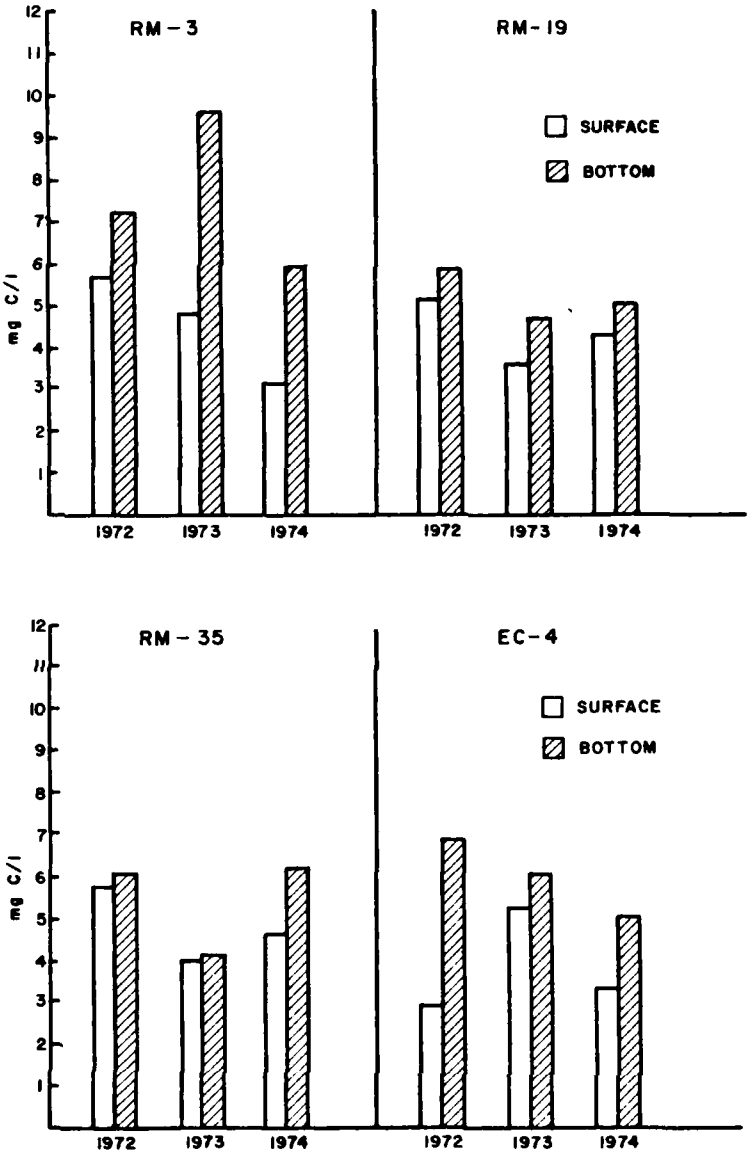


Figure 3. Mean soluble carbon levels at RM-3, RM-19, RM-35, and EC-4 during the three sampling years

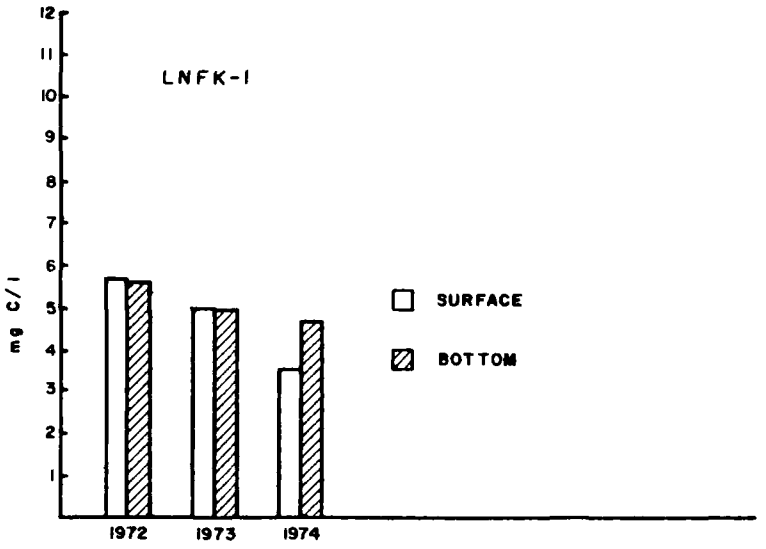
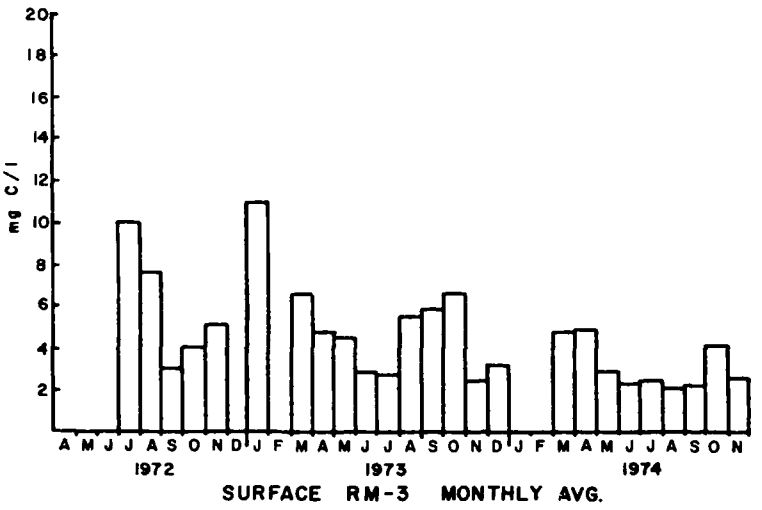


Figure 3 (continued). Mean soluble carbon level at LNFK-1 during the three sampling years



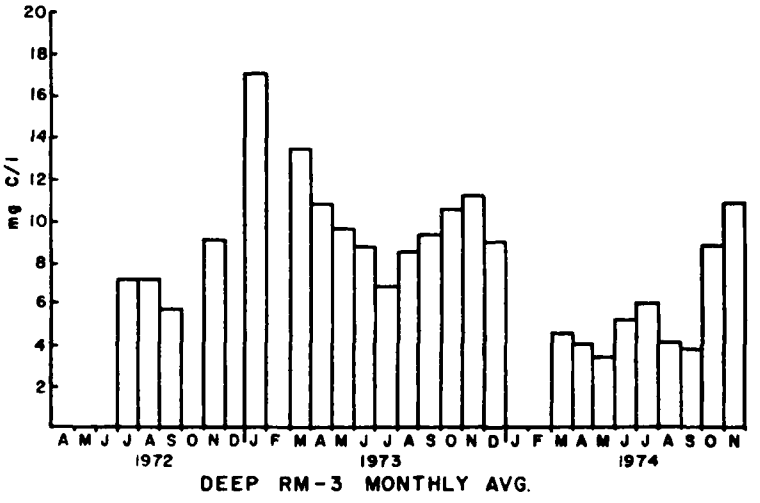


Figure 4. Monthly mean soluble carbon levels at RM-3

Mean dry weights
(mg/l)

Month	Control	1.0 N	0.01 P	0.05 P	N + P	Monthly mean dry wt.
Oct	0.18	0.17	1.86	2.18	6.78	0.97
Mar	1.51	0.43	1.45	1.59	5.75	1.55
Apr	1.35	1.91	2.63	2.45	5.37	2.45
May	0.13	0.12	1.35	1.03	8.71	0.75
Jul	0.25	0.14	1.55	1.63	7.76	0.93

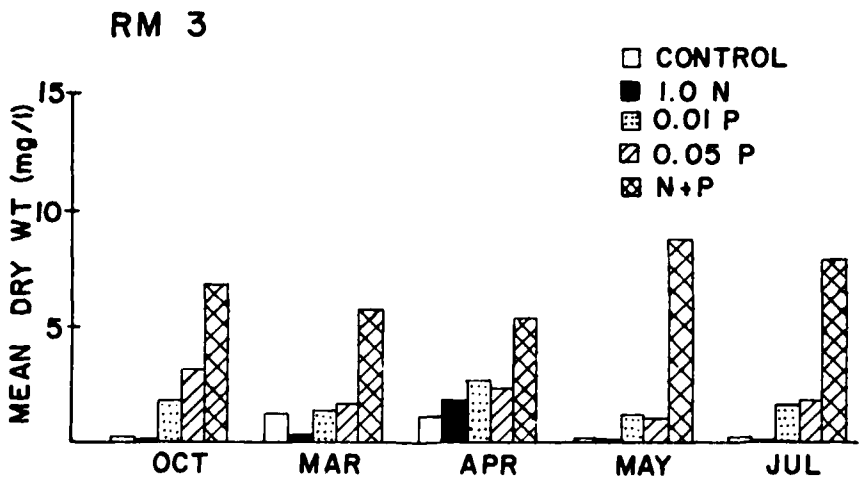


Figure 5. Mean dry weight and nutrient stimulation comparisons of growth in RM-3 algal assays

Mean dry weights
(mg/l)

Month	Control	1.0 N	0.01 P	0.05 P	N + P	Monthly mean dry wt.
Oct	0.23	0.25	1.91	1.95	7.25	1.10
Mar	0.71	0.19	1.03	1.11	2.24	0.81
Apr	1.21	1.86	2.57	2.45	7.24	2.51
May	0.64	0.58	1.48	1.48	7.59	1.45
Jul	0.26	0.22	1.70	1.78	7.94	1.07

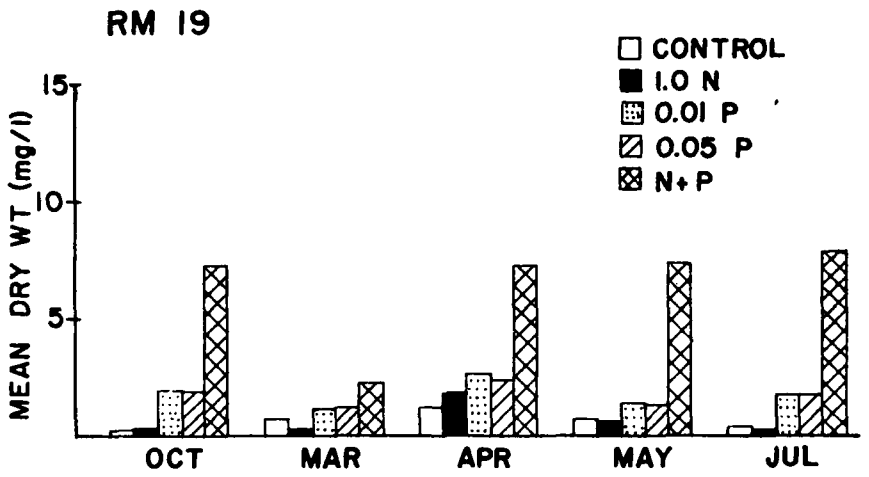


Figure 6. Mean dry weight and nutrient stimulation comparisons of growth in RM-19 algal assays

Mean dry weights
(mg/l)

Month	Control	1.0 N	0.01 P	0.05 P	N + P	Monthly mean dry wt
Oct	0.97	0.30	1.82	2.09	4.57	1.38
Mar	0.72	0.40	1.82	1.38	6.16	1.38
Apr	1.12	1.23	2.09	2.09	8.13	2.19
May	0.51	0.69	0.49	0.67	7.59	0.97
Jul	0.37	0.24	1.41	1.41	8.71	1.07

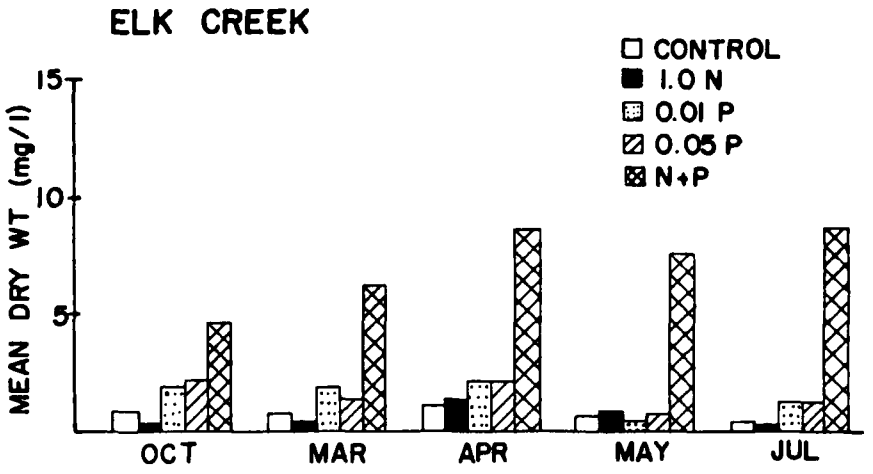


Figure 7. Mean dry weight and nutrient stimulation comparisons of growth in EC-4 algal assays

Mean dry weights
(mg/l)

Month	Control	1.0 N	0.01 P	0.05 P	N + P	Monthly mean dry wt
Oct	0.12	0.11	1.41	1.20	4.79	0.64
Mar	----	----	----	----	----	---
Apr	0.79	1.29	2.29	1.95	8.51	2.09
May	0.09	0.10	1.03	1.10	7.94	0.61
Jul	0.15	0.12	1.26	1.07	7.76	0.72

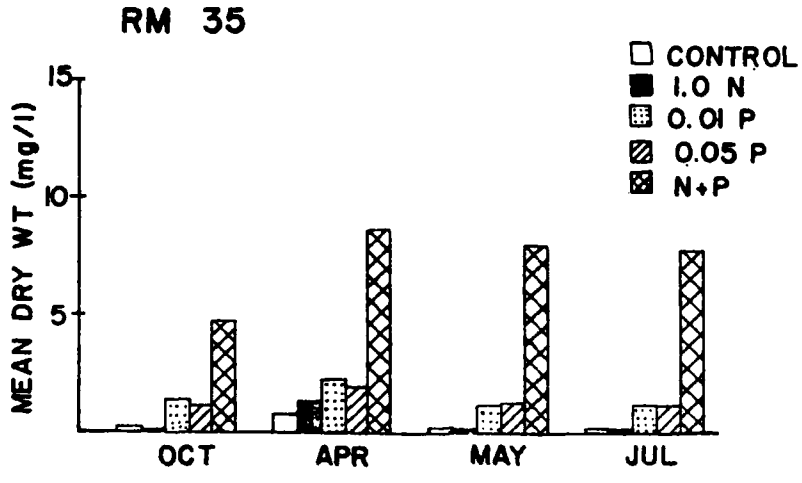


Figure 8. Mean dry weight and nutrient stimulation comparisons of growth in RM-35 algal assays

Mean dry weights
(mg/l)

Month	Control	1.0 N	0.01 P	0.05 P	N + P	Monthly mean dry wt
Oct	0.12	0.14	1.05	0.83	3.55	0.55
Mar	----	----	----	----	----	----
Apr	4.07	11.50	3.63	3.63	10.70	5.76
May	0.26	0.30	1.95	1.78	7.24	1.15
Jul	0.15	0.10	1.07	1.07	8.51	0.69

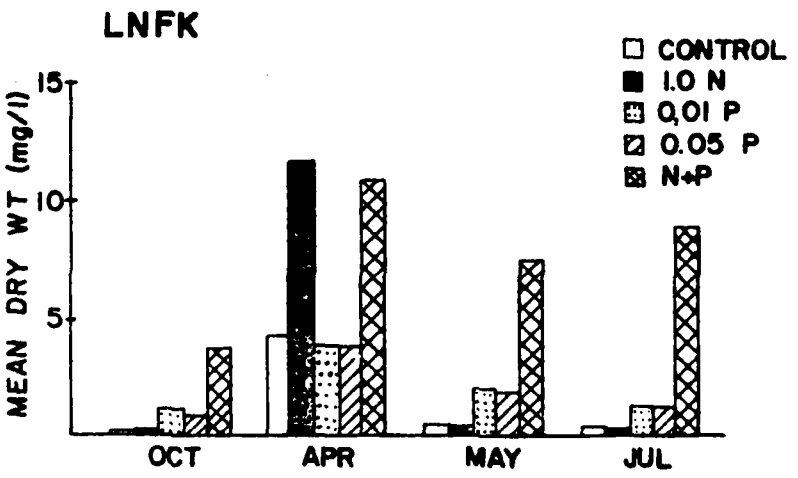


Figure 9. Mean dry weight and nutrient stimulation comparisons of growth in LNFK-1 algal assays

F-test and analysis of variance, verified the experimental data presented in the following graphs and tables.

Results for RM-3 are shown in Fig. 5 and in Figs. 10-14. Phosphorus was the nutrient limiting algal growth at RM-3 in all assays made. Maximum yield ranged from a low of 13.80 mg algal dry wt/1 to a high of 23.0 mg algal dry wt/1. In several cases (March, May, and July 1975) there appeared to be a slight decrease compared with the control flasks in algal dry weight produced with a 1.0 mg/1 N addition. This decrease was probably the result of increased bacterial activity in those flasks; the bacteria were better able to utilize the available nutrients and so outgrew the algae.

Maximum biomass for RM-19 ranged from 1.76 to 19.8 mg algal dry wt/1. Phosphorus was the nutrient limiting algal growth in all cases except in the March 1975 assay when the maximum yield was only 2.76 mg algal dry wt/1. These data suggest that algal growth was limited by some element other than nitrogen or phosphorus during this sample period. Results for the RM-19 are shown in Fig. 6 and in Figs. 15-19.

Both phosphorus and nitrogen were necessary to support increased growth in March and May 1975 assays on Elk Creek samples (Figs. 21 and 23). Phosphorus alone was the limiting nutrient in all other cases (Figs. 20, 22, 24). The range of the maximum yield was 15.50 to 21.30 mg/1. The results of the assays from EC-4 can be seen in Fig. 7.

In general, algal dry weights obtained in algal assays on water samples from RM-35 tended to be lower than those from the previous three sites discussed. The extremely low mean dry weight values for

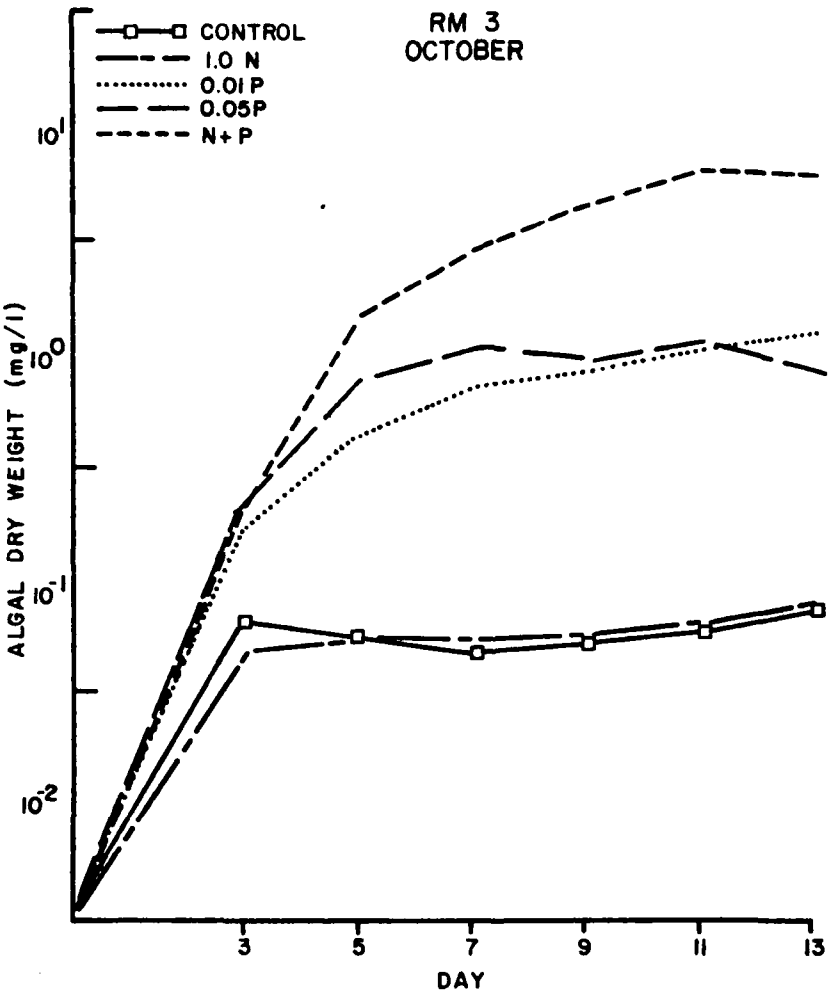


Figure 10. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in October 1974

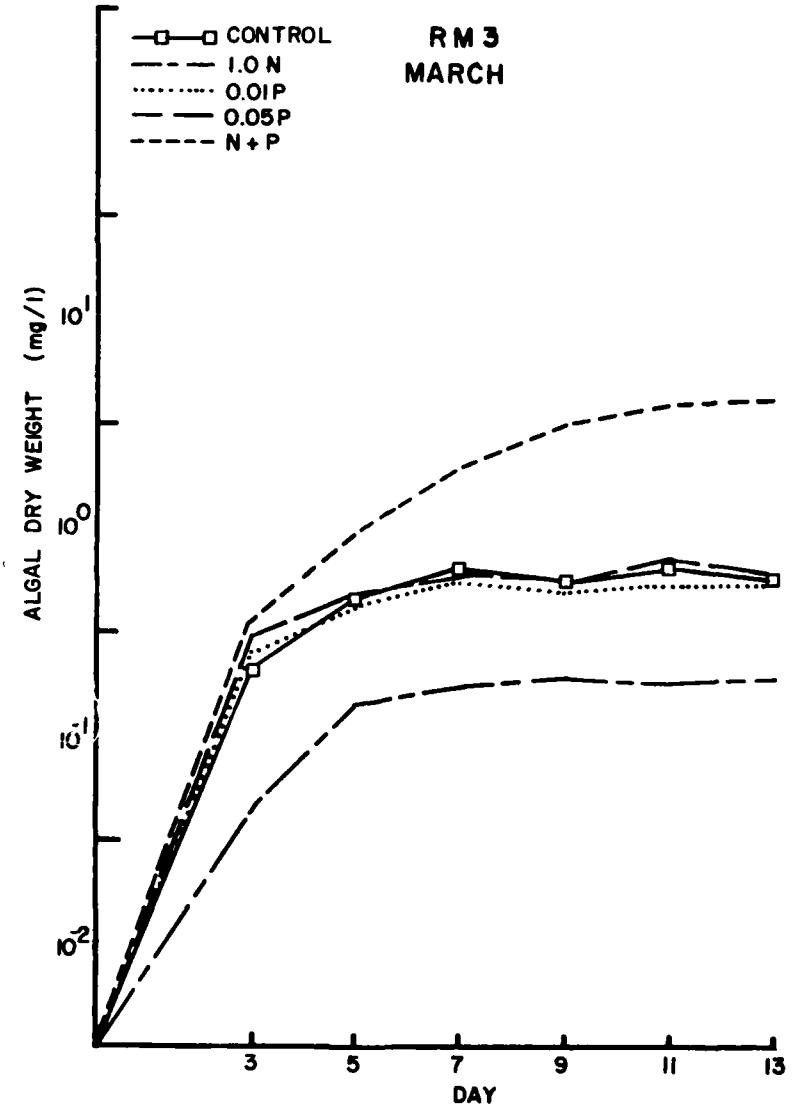


Figure 11. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in March 1975

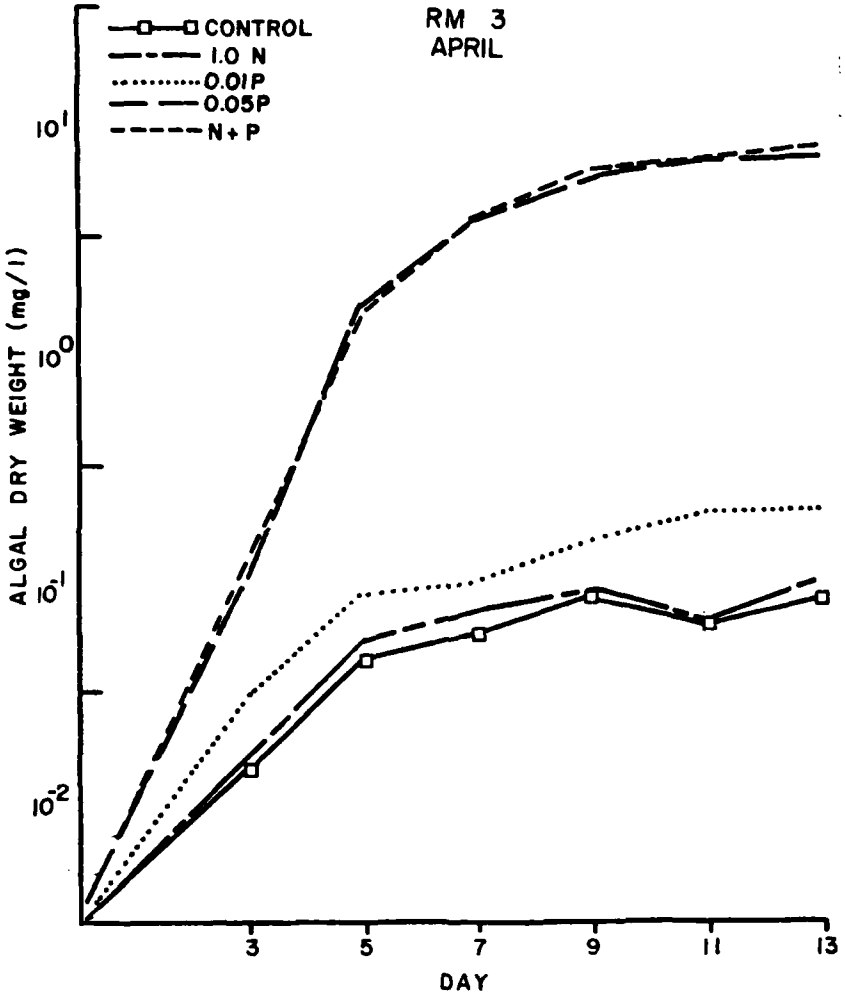


Figure 12. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in April 1975

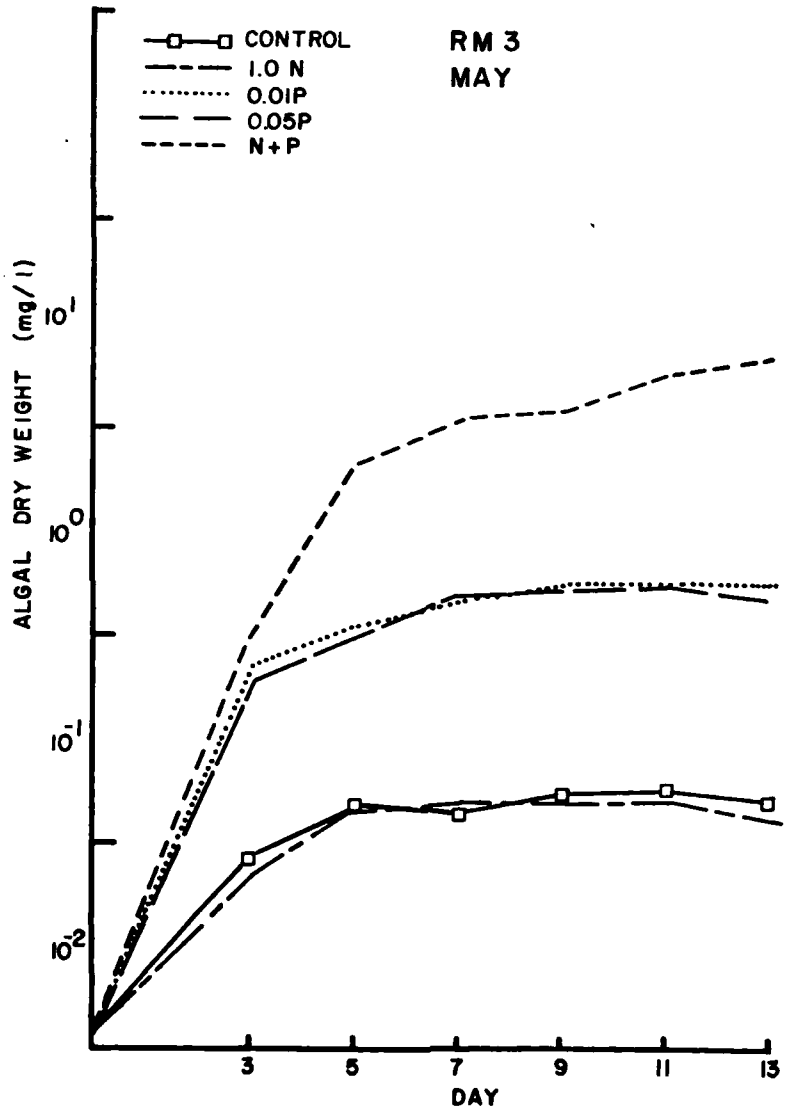


Figure 13. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in May 1975

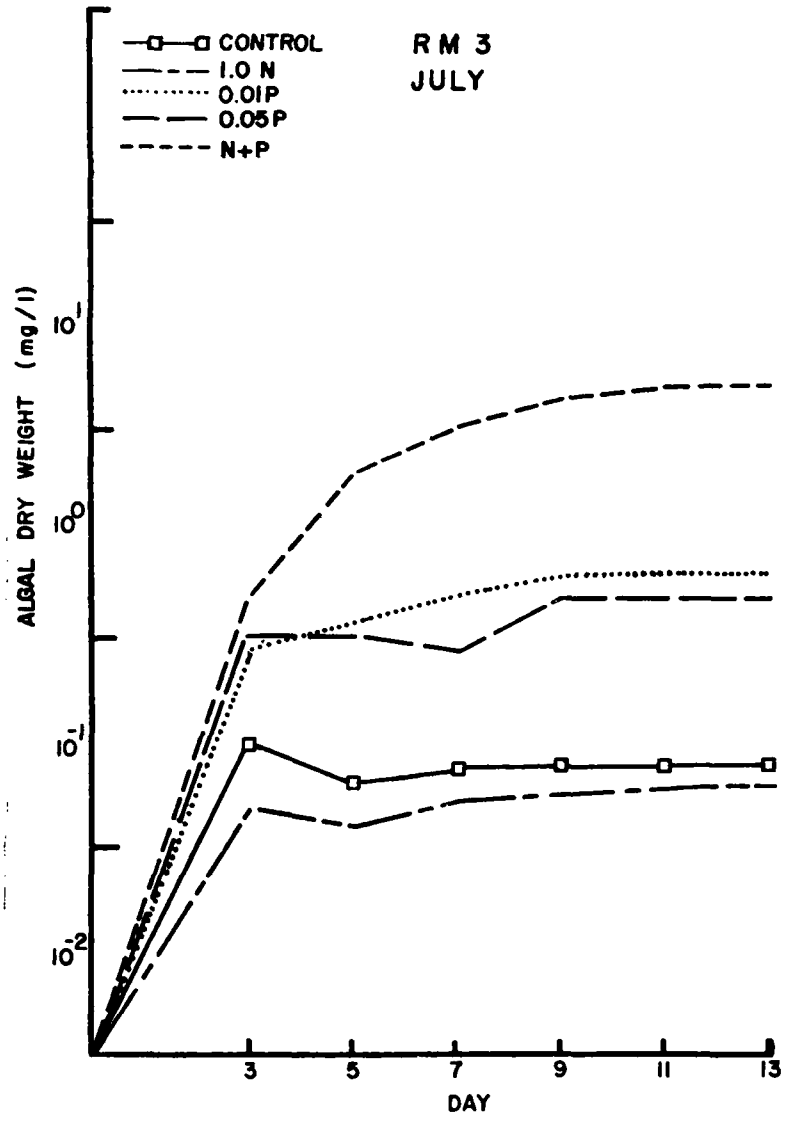


Figure 14. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-3 in July 1975

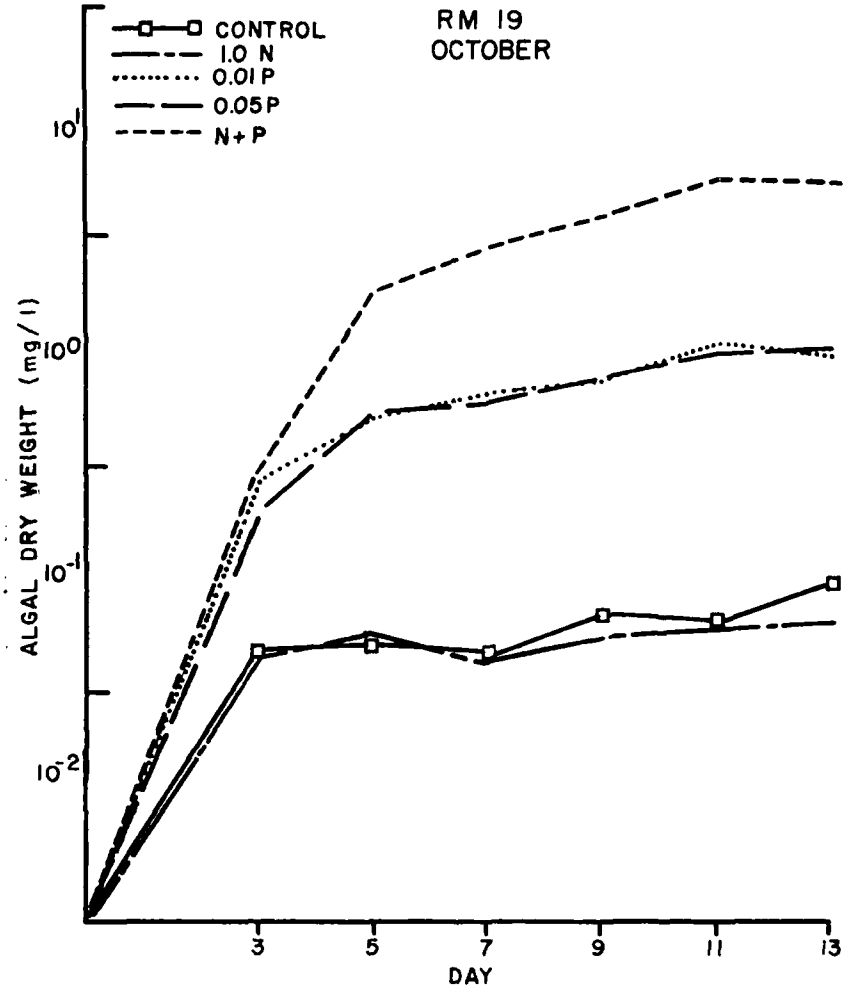


Figure 15. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in October 1974

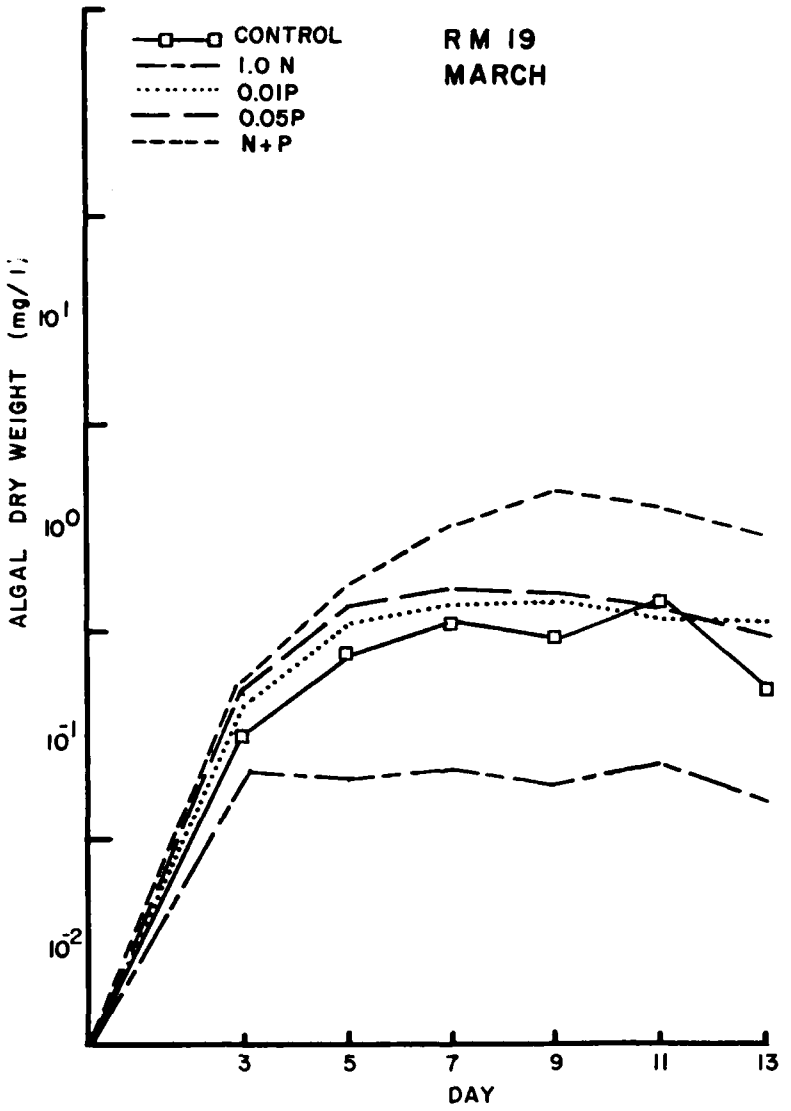


Figure 16. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in March 1975

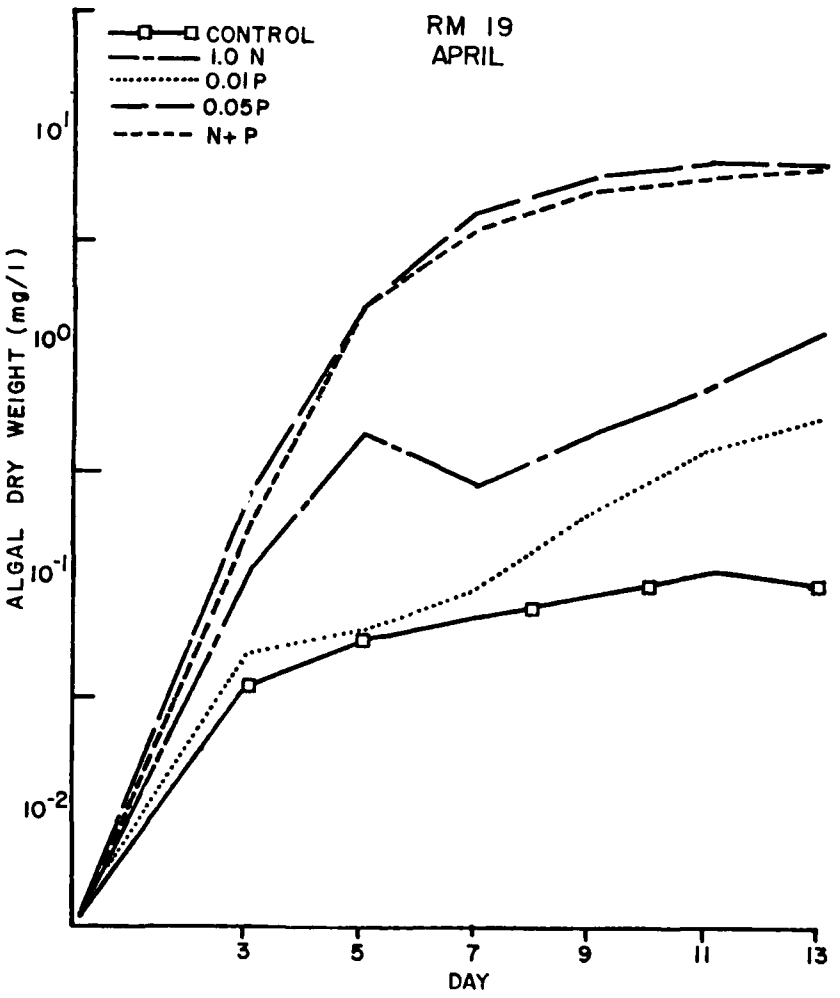


Figure 17. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in April 1975

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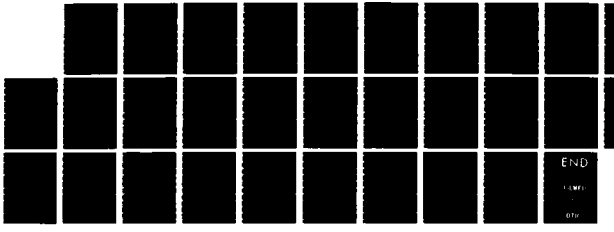

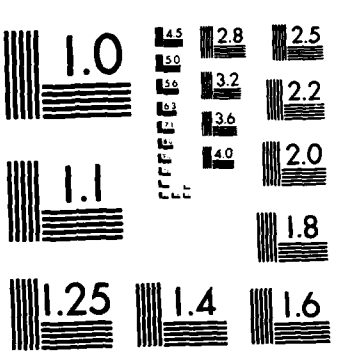

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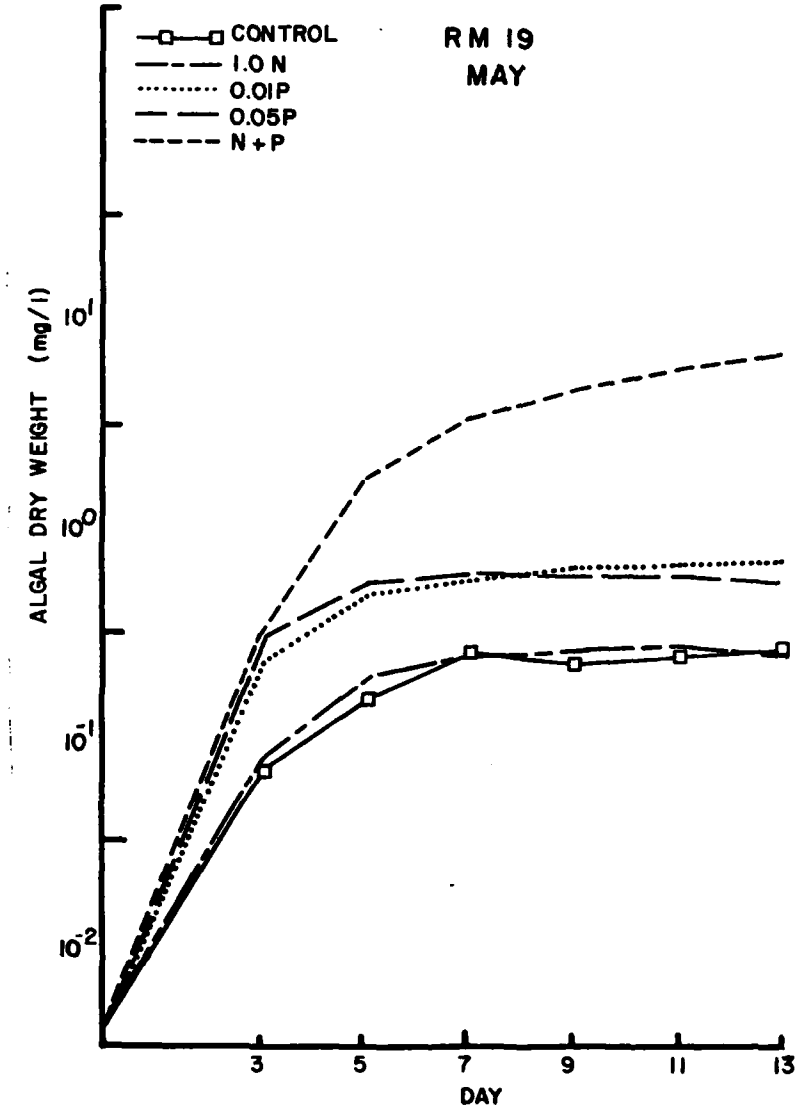

Figure 18. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in May 1975

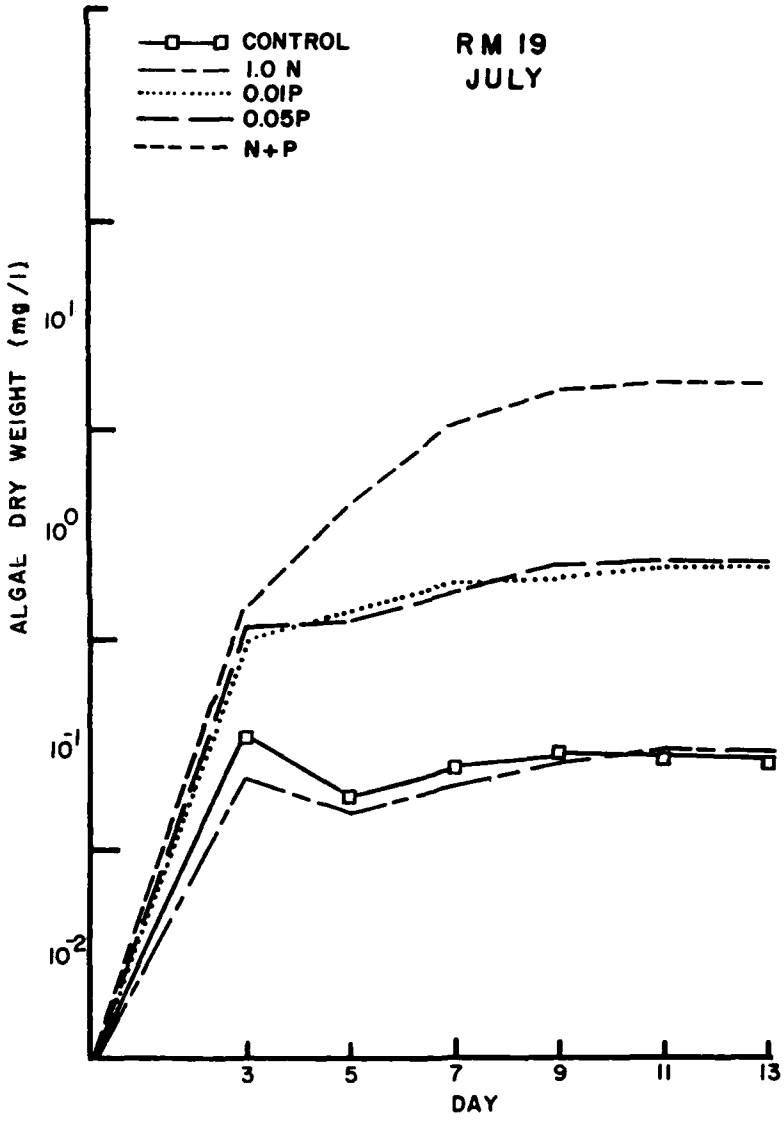

Figure 19. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-19 in July 1975

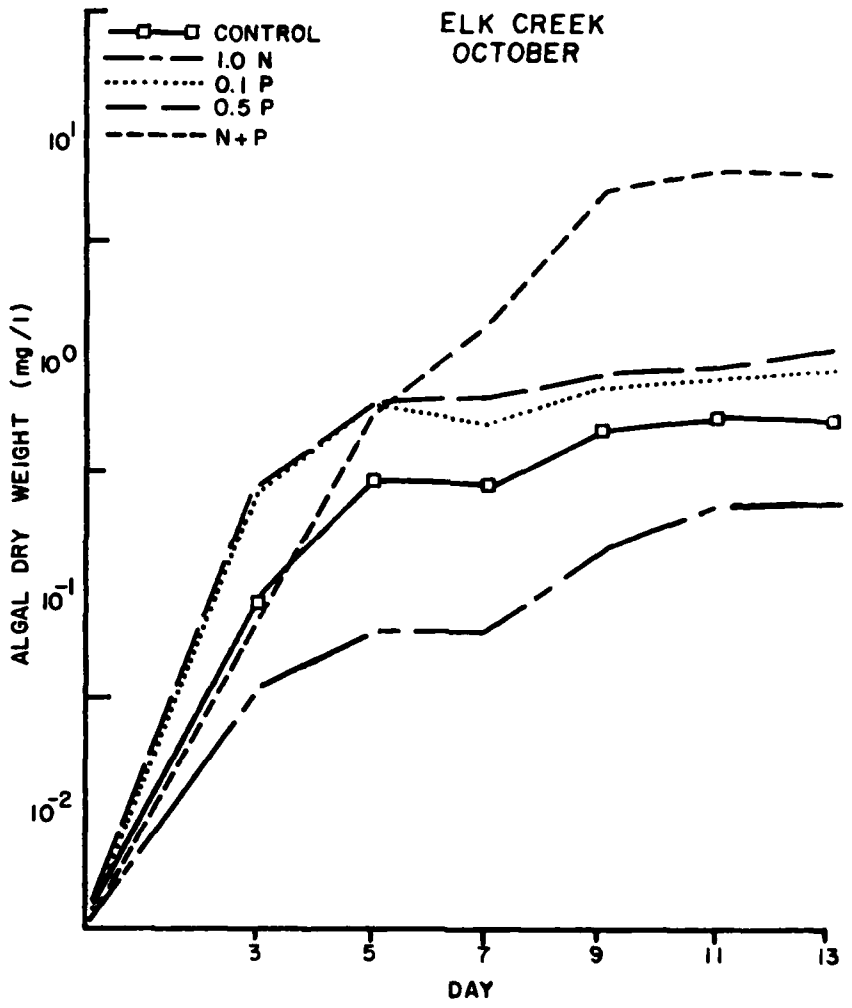

Figure 20. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in October 1974

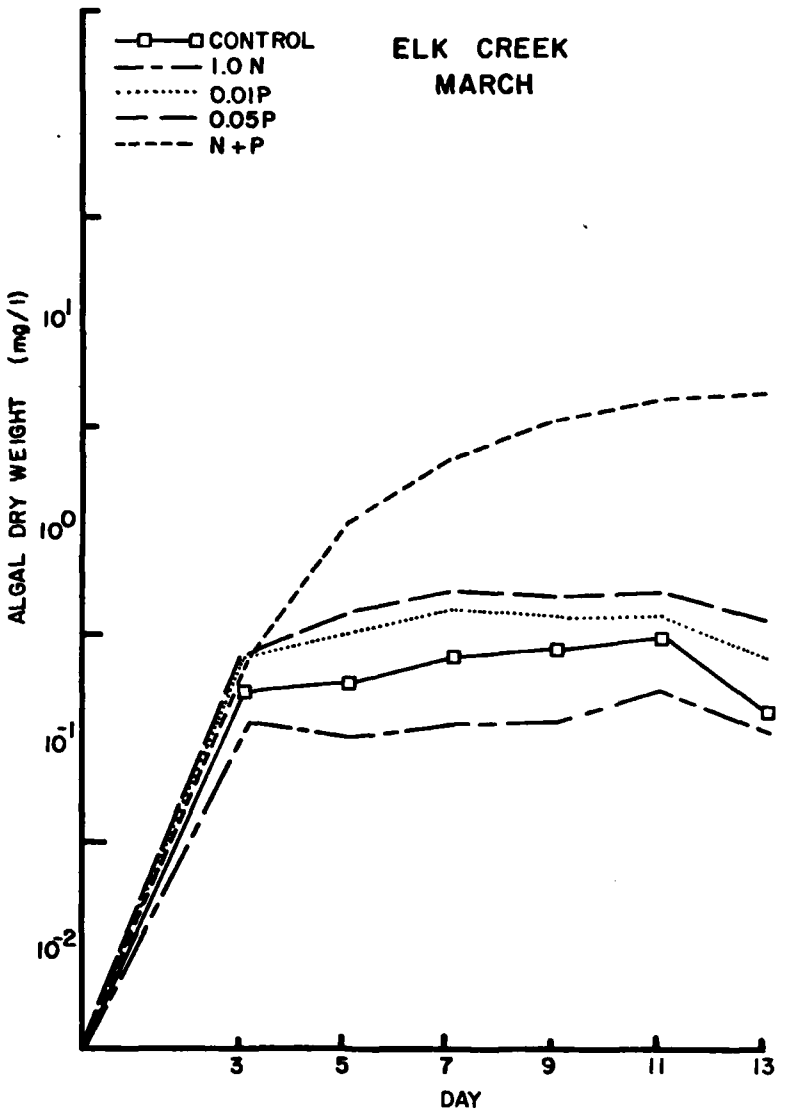

Figure 21. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in March 1975

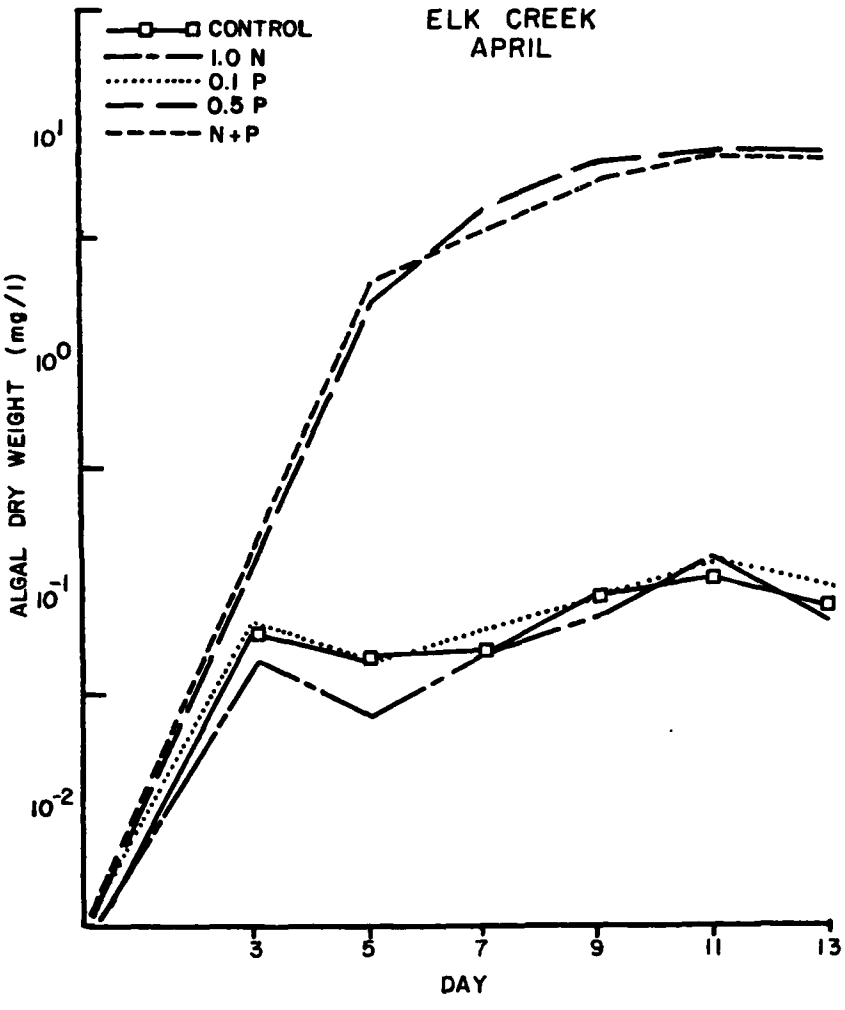

Figure 22. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in April 1975

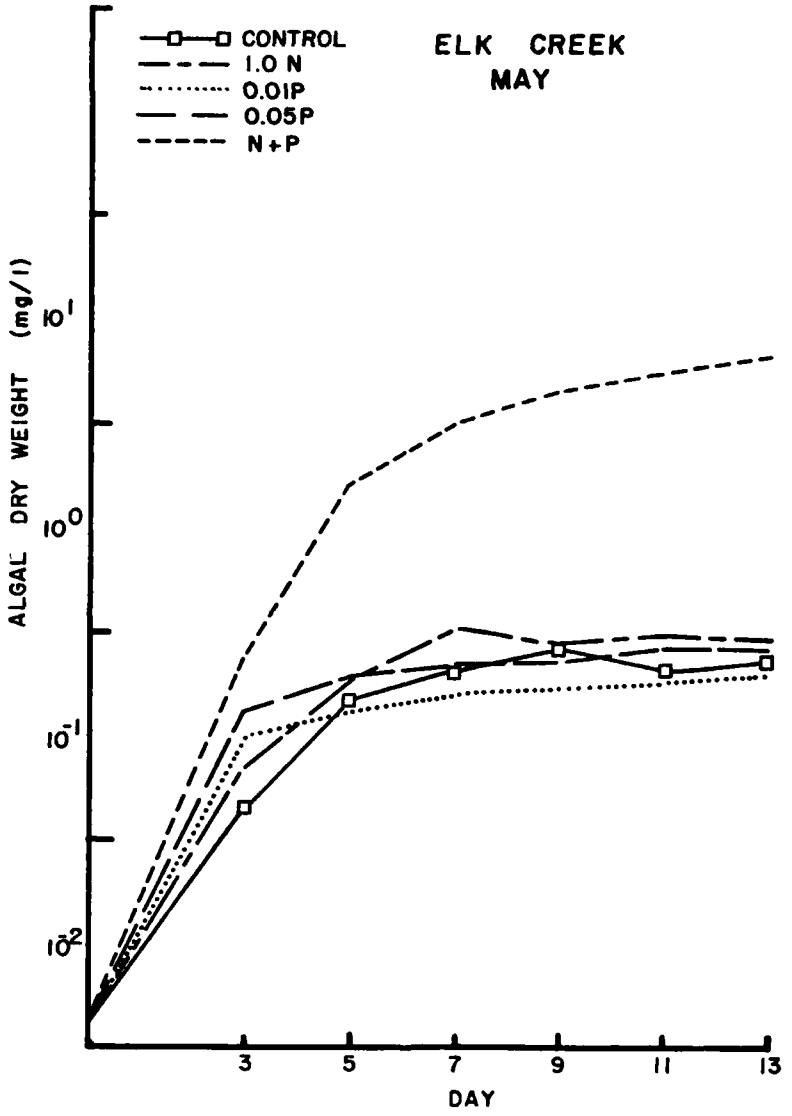

Figure 23. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in May 1975

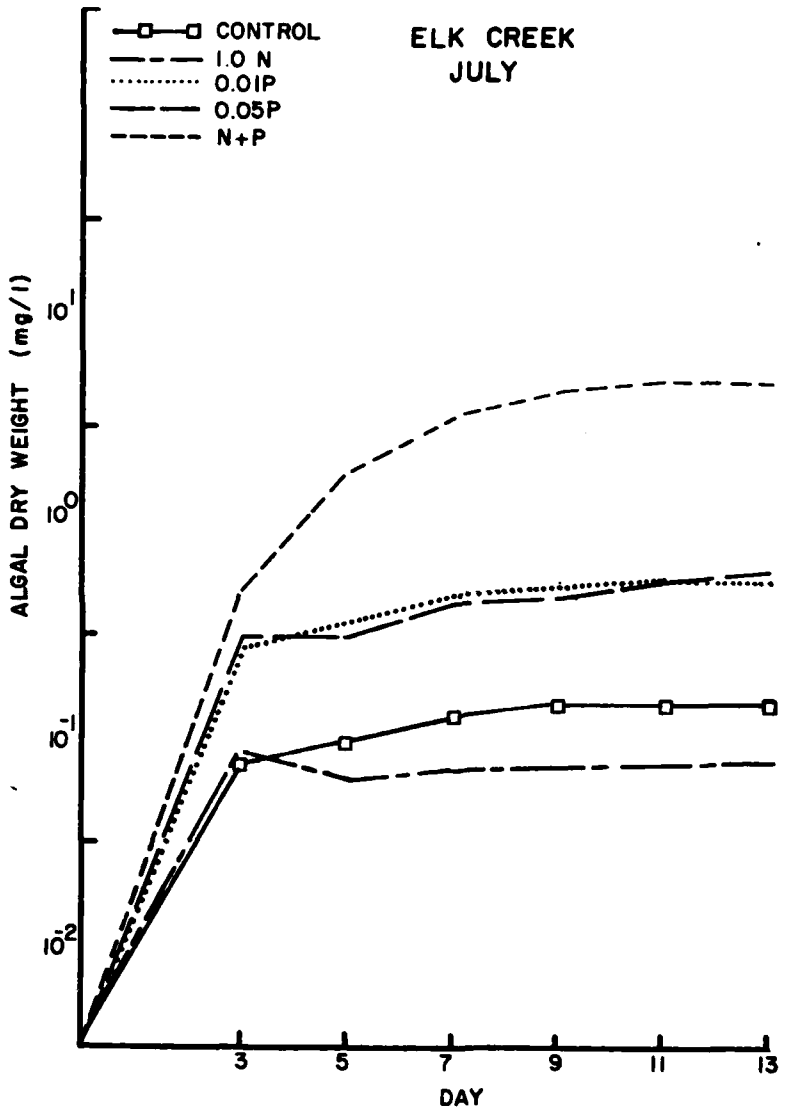

Figure 24. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from EC-4 in July 1975

the October 1974 control flasks (Fig. 8) indicate a low level of intrinsic nutrients present in the sample. The sharp increases in dry weight in the April 1975 assays over those for October may have been the result of the increased availability of phosphorus. Algal growth was limited by the phosphorus concentration in all the assays on RM-35 water samples. The maximum yield was from 14.00 to 19.30 mg algal dry wt/l. Results of the assays are shown in Figs. 25-28.

Phosphorus was the nutrient limiting algal growth in the October 1974, May and July 1975 assays at LNFK-1 (Figs. 29, 31, 32). April 1975 assays in LNFK-1 gave significantly higher results than those from any other assay (Fig. 30). Little or no increase in dry weight produced was noted with 0.01 and 0.05 mg/1 P additions over the control (Fig. 30). There was no significant difference between dry weight obtained with the 1.0 mg/1 N and the N + P additions. This result, in conjunction with the extremely high mean dry weight obtained with the 1.0 ml/1 N addition (Fig. 9), indicates that nitrogen was the limiting nutrient for algal growth in April. Maximum yield ranges from a 12.00 mg/1 low to a high of 22.50 mg algal dry wt/1.

Some general trends emerged from the assays. The monthly mean dry weight (Figs. 5-9) indicated that for all five sites the highest productivity values were obtained in the April assays. Cold water temperatures and inclement weather were prevalent in the winter of 1974-75 so April coincided with the time of minimal productivity. Algal assays on Dworshak Reservoir samples agree closely with predicted

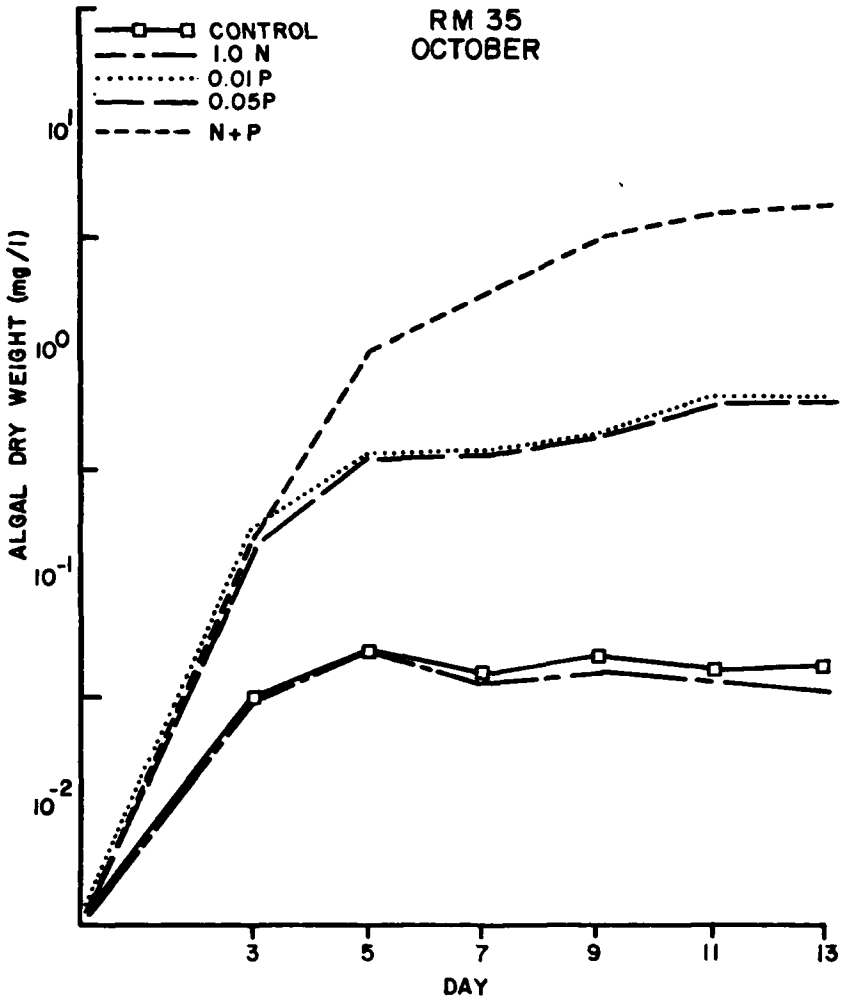

Figure 25. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in October 1974

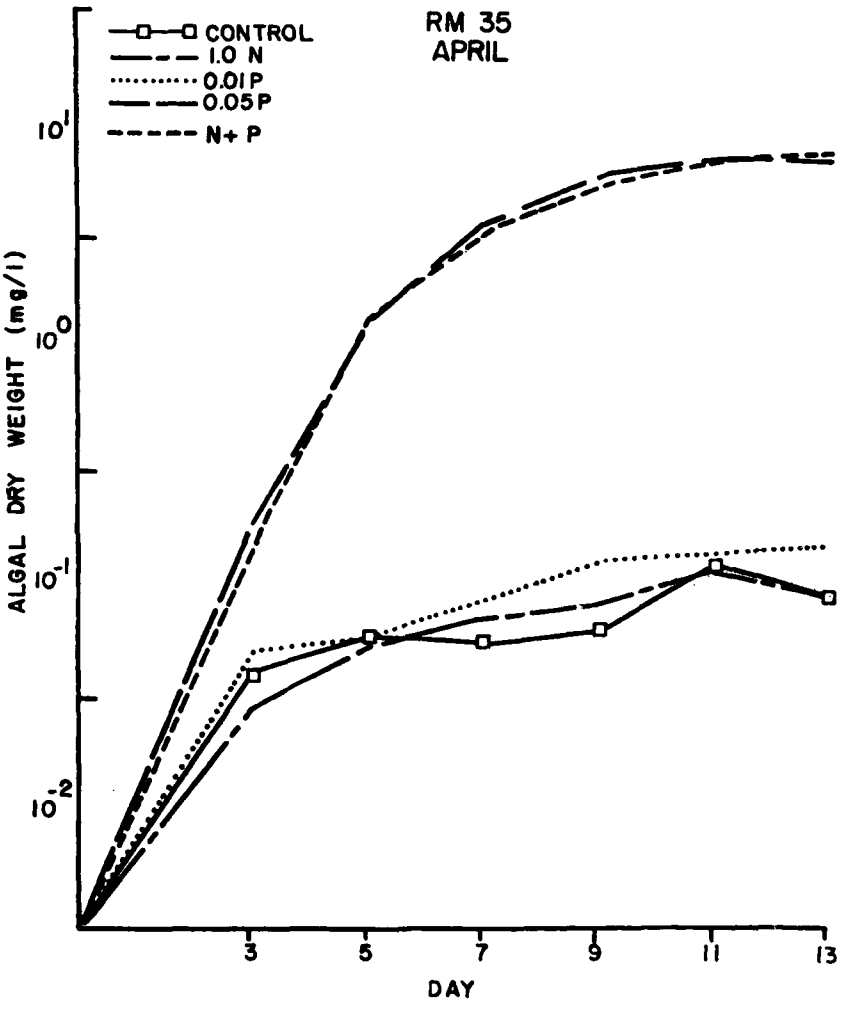

Figure 26. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in April 1975

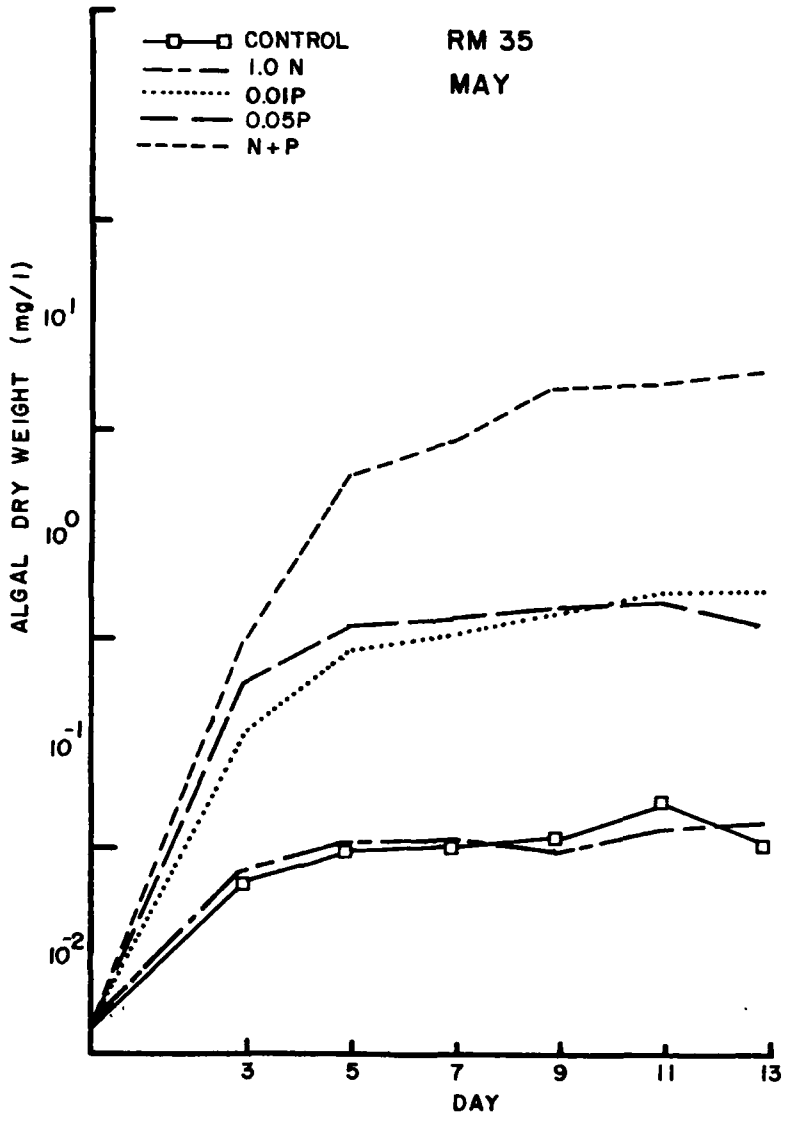

Figure 27. The effect of phosphorus and nitrogen addition on the growth of Selenastrum capricornutum in water from RM-35 in May 1975

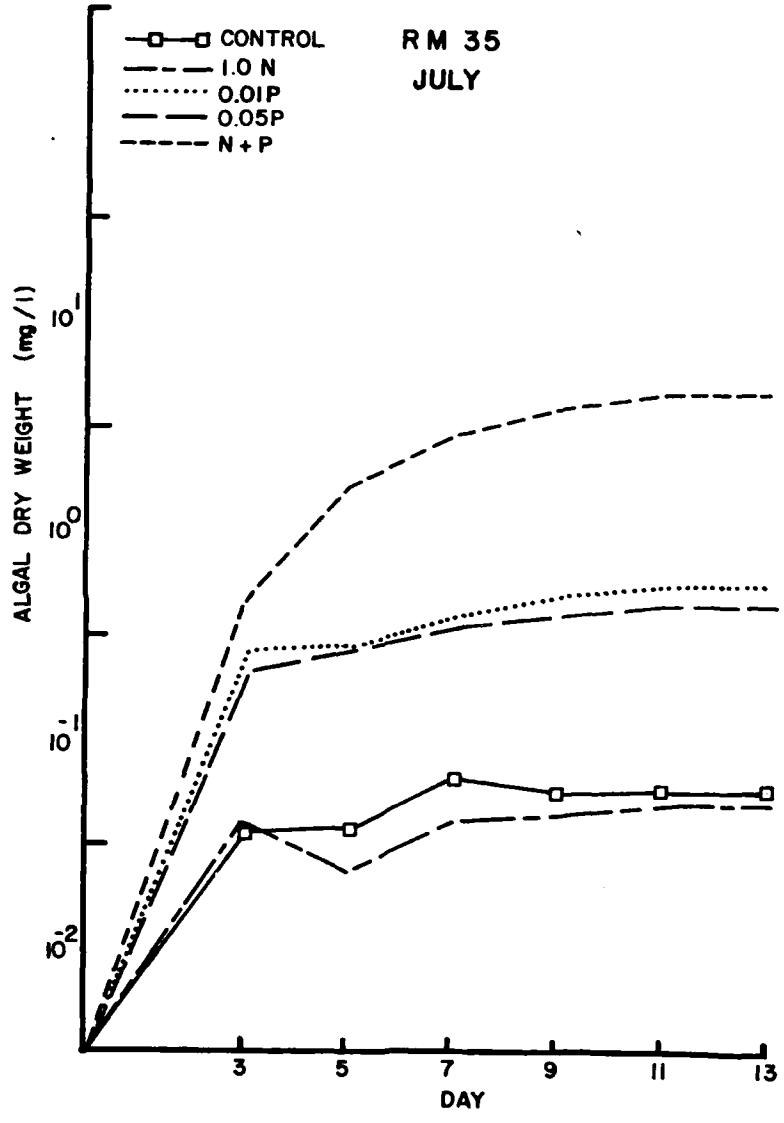

Figure 28. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from RM-35 in July 1975

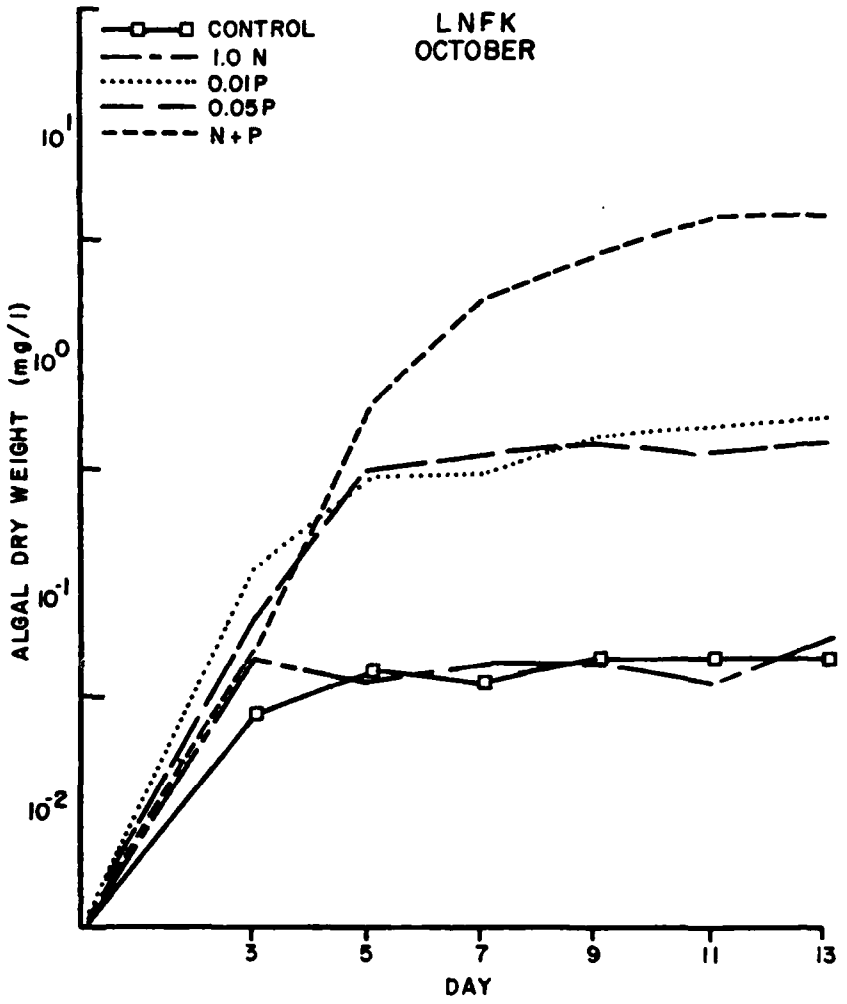

Figure 29. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in October 1974

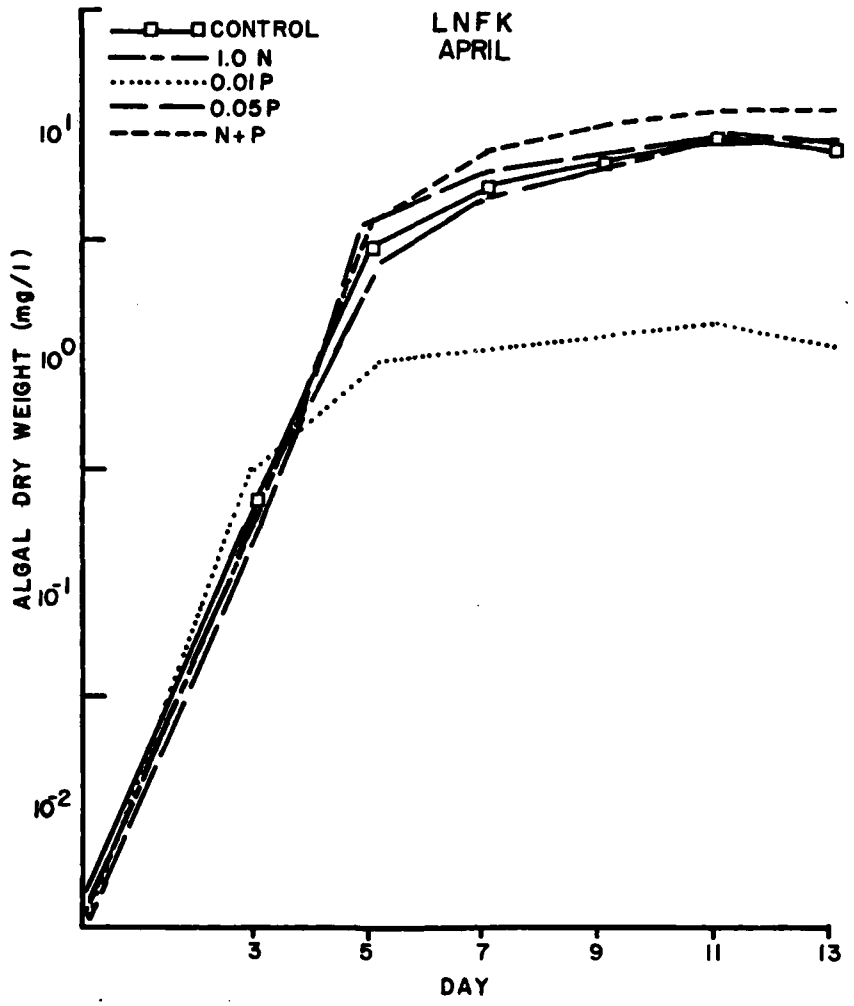

Figure 30. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in April 1975

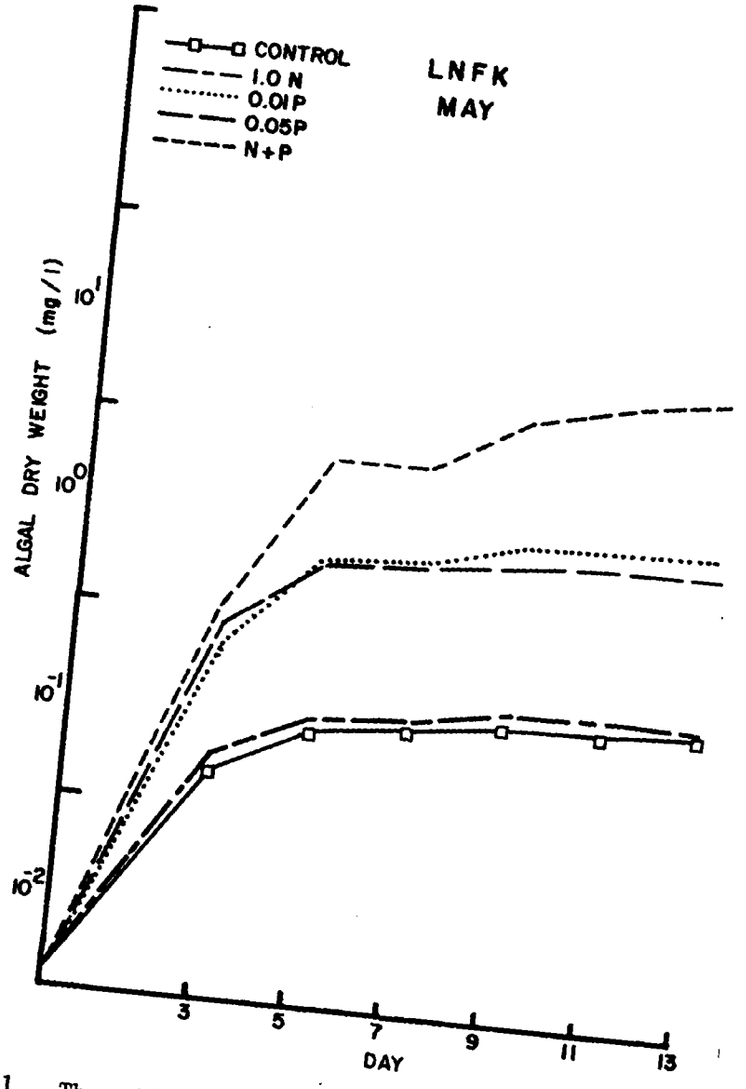

Figure 31. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in May 1975

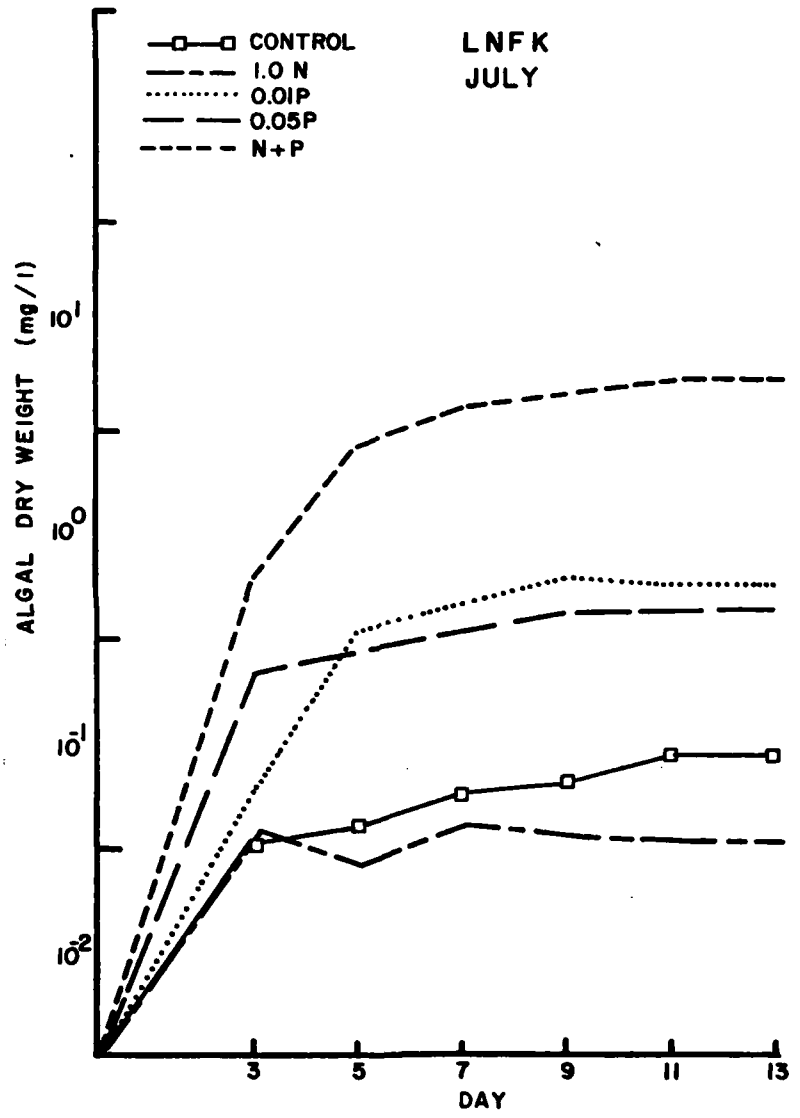

Figure 32. The effect of phosphorus and nitrogen addition on growth of Selenastrum capricornutum in water from LNFK-1 in July 1975

seasonal fluctuations in productivity and nutrient concentrations discussed in classic limnological theory (9).

Results of algal assays on three of the five sites showed a seasonal low in mean dry weight in the month of May. Samples from RM-3, EC-4, and RM-35 were taken at the end of May when water levels in the reservoir were extremely low. Spring algal blooms, in concert with the lack of a nutrient-enhancing spring runoff, were probably the cause of the low production values in May. The October seasonal low obtained in assays on LNFK-1 samples was probably the result of depletion of nutrients by the fall algal bloom.

Seasonal fluctuations in nutrient concentrations as illustrated by the assay appeared to agree with established limnological theory (9). In general, nutrient concentrations were high in winter and early spring and low in summer and late fall. Maximum potential algal biomass produced at all sites was similar throughout the reservoir, ranging from an average low of 12 mg/l to a high of 23 mg/l dry weight, while natural production levels were in the range of 0.55 to 5.76 mg dry wt/l.

These results indicated that phosphorus was generally the nutrient limiting algal growth. In nearly all cases addition of phosphorus alone to experimental flasks resulted in an increase in algal biomass over control levels, while addition of both phosphorus and nitrogen compounds gave significant increases in dry weight yields. The latter result suggests nitrogen may have a limiting effect on algal growth at higher phosphorus levels. Another study (19) has verified that phosphorus is limiting in algal assays on water from Dworshak Reservoir.

The relative extent of phosphorus limitation varied seasonally. During algal bloom periods in late summer and fall both nitrogen and phosphorus were present in low concentrations. Due to the high organismal phosphorus concentrations to environmental phosphorus concentration this element rapidly became limiting to algal growth. Seasonal fluctuations in phosphorus concentrations in the reservoir were reflected in the varying algal dry weights produced in the assays and in the rate at which nitrogen became growth limiting in relation to phosphorus. As concentrations of both nutrients increased the probability of growth limitation by nitrogen rather than phosphorus also increased (LNFK-1, April 1975).

According to a study by Miller et al. (10), four productivity groups for lake waters can be defined, based on algal biomass obtained in various lake waters. They are: low productivity (0.00-0.10 mg dry wt/1), moderate productivity (0.11-0.80 mg dry wt/1), moderately high productivity 0.81-6.00 mg dry wt/1), and high productivity (6.10-20.00 mg dry wt/1). As indicated by monthly mean dry weights obtained in algal assays on Dworshak Reservoir (Figs. 5-9), this ecosystem would be classified as one of moderate productivity. Studies by Ferris et al. (11) and Payne (12) showed that addition of nutrients to oligotrophic and mesotrophic waters resulted in significant algal growth increases while causing little change when added to eutrophic waters. Since Dworshak Reservoir is considered oligo-/mesotrophic with moderate productivity, any nutrient inputs to the reservoir would probably result in significant production of algae. If phosphorus levels in

the reservoir were artificially increased by allocthonous materials, primary production would increase to a point such that nitrogen limitation would become a factor regulating growth. If both nitrogen and phosphorus concentrations in the reservoir were to increase, then significant algal growth increases would result. After a certain level of high fertility and high productivity was reached no further significant biomass increases would result from continued nutrient input.

These conclusions are supported by the data from the National Eutrophication Survey (L. R. Williams, S. C. Hern, EMSL, EPA, Las Vegas, pers. comm.). Using Vollenweider's (13) loading rates for phosphorus, it was estimated that Dworshak's loading rate for phosphorus was 1.50 $g/m^2/yr$. Vollenweider's rates indicate that the "eutrophic" loading for Dworshak would be 1.56 $g/m^2/yr$ while the "oligotrophic" loading rate would be 0.78 $g/m^2/yr$. From these data it can be predicted that increased phosphorus loads of any consequence would lead to rapid acceleration towards the eutrophic state if other nutrients are available.

Survival of Indicator Organisms in Dworshak Water: Since coliforms were constantly found in the reservoir and appeared to be growing in the system rather than being introduced, the growth and survival rates of these organisms became significant.

In an attempt to simulate natural death rates in the reservoir, microorganisms, in membrane chambers that contained filtered or unfiltered lake water as the supporting medium, were submerged in the Dworshak Reservoir. This experiment was terminated after 7 days, due

to vandalism of the membrane chambers. However, prior to the loss of the chambers, noteworthy death rates were observed (Fig. 33).

All organisms, in the membrane chambers containing filtered water, demonstrated an initial erratic growth and death pattern. E. coli exhibited only subtle changes in numbers, increasing from 7.5 x 10^5 cells/ml to 2.5 x 10^6 cells/ml in the first day. S. faecalis var. liquefaciens, E. aerogenes, and the Salmonella all demonstrated significant growth during the first day. S. faecalis var. liquefaciens increased from 8.0 x 10^6 cells/ml to 7.8 x 10^8 cells/ml, nearly a 100-fold increase. Both E. aerogenes and the Salmonella showed greater than a 10-fold increase. By the third day of sampling, all organisms had declined to their original numbers. After 7 days, none of the organisms had decreased more than 90%. This extended survival time was also noted in the laboratory experiments that employed Dworshak water as the supporting medium where, after 7 days, all organisms were present in nearly the same numbers as they were at initiation of the experiment. Obviously, then, the survival of the microorganisms was similar in the laboratory and field experiments.

In the membrane chambers filled with unfiltered reservoir water, all of the microorganisms experienced a period of erratic behavior upon introduction into the membrane chambers. Similar to the increases noted in the filtered water, E. coli increased the least of all the organisms, from 7.5 x 10^5 to 2.0 x 10^6 cells/ml (E. aerogenes, S. faecalis var. liquefaciens, and the Salmonella all increased 10- to 100-fold the first day). A subsequent reduction was then observed for

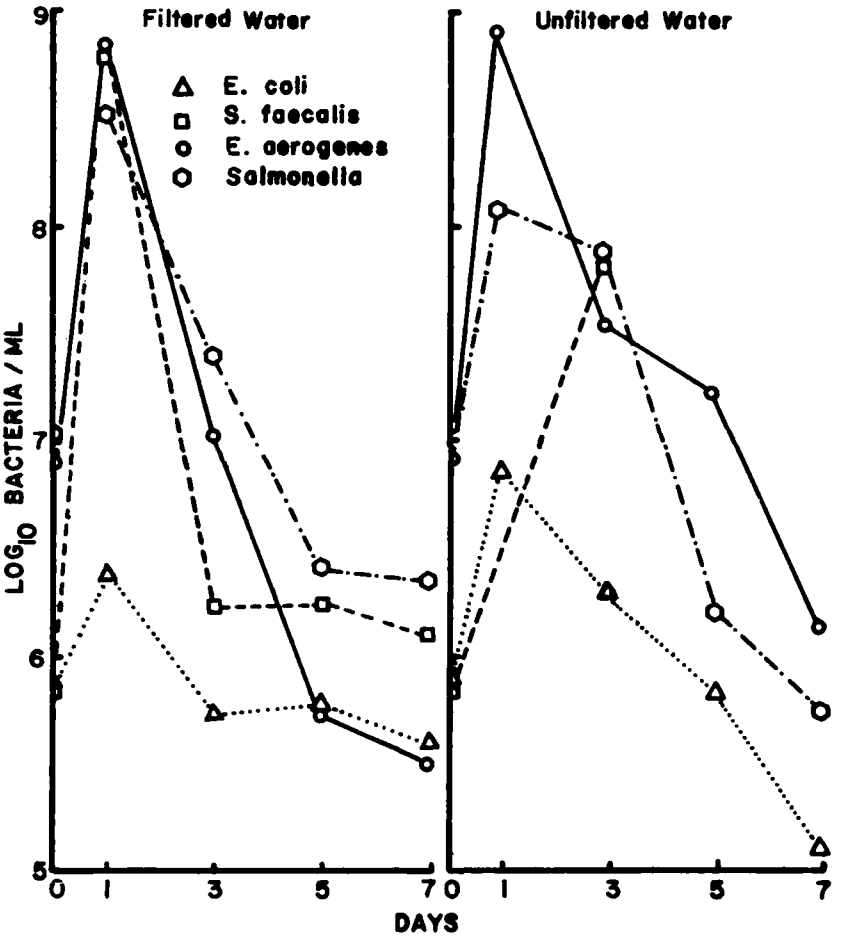

Figure 33. Survival rates of selected indicator organisms in filtered and unfiltered Dworshak water, 20 July 1973

all species. Rates of the reduction in the unfiltered water were more rapid than in the filtered water.

The above experiment was repeated and death rates of the microorganisms were monitored for 28 days in the Dworshak Reservoir using similar membrane chambers and supporting media.

In the filtered water chambers, in contrast with other experiments, only E. aerogenes and Salmonella exhibited erratic behavior (showing slight initial increases) whereas E. coli and S. faecalis var. liquefaciens numbers remained stable during the initial sampling period (Fig. 34). Later, S. faecalis var. liquefaciens decreased rapidly, declining from 1.0×10^7 to 3.0×10^3 cells/ml in 14 days. This decrease was dissimilar to the death rate observed in the filtered reservoir water laboratory experiment. After the 15th day S. faecalis var. liquefaciens could no longer be detected.

E. coli exhibited a rate similar to past investigations, to approximately 1.0×10^3 organisms/ml after 20 days, and then maintaining a constant concentration for the remaining 7 days. Both E. aerogenes and Salmonella numbers declined steadily to approximately 2.0×10^4 microorganisms/ml after 27 days. Their 7-day death rates were similar to the previous field experiment, but E. aerogenes declined more rapidly than it did in the filtered reservoir water laboratory experiment.

In the unfiltered water chambers all microorganisms again showed an initial erratic behavior with E. aerogenes increasing from 1.0×10^7 to 3.2×10^9 cells/ml in 24 h (Fig. 35). All species

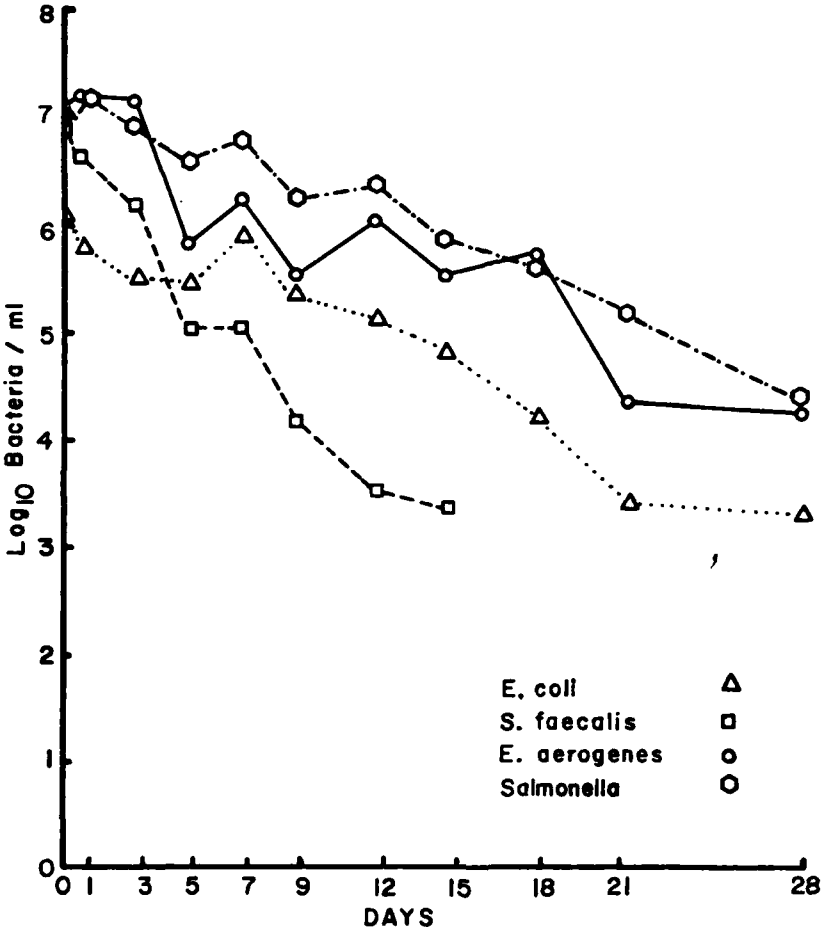

Figure 34. Survival of Escherichia coli, Streptococcus faecalis var. liquefaciens, Enterobacter aerogenes, and a Salmonella sp. in filtered Dworshak water, 3 August 1973

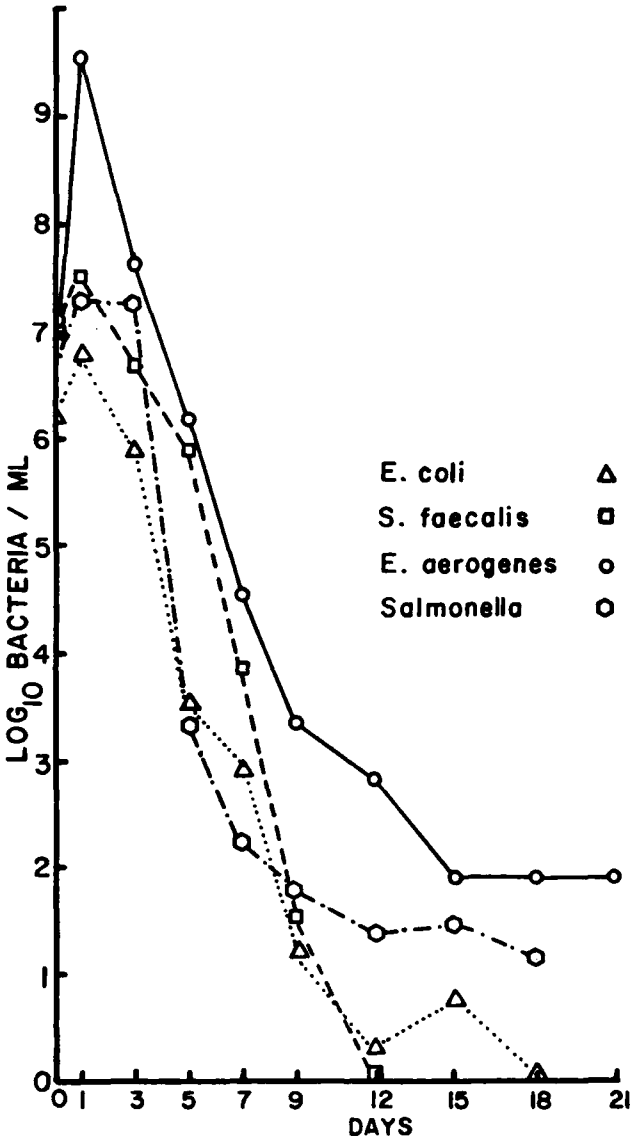

Figure 35. Survival of Escherichia coli, Streptococcus faecalis var. liquefaciens, Enterobacter aerogenes, and a Salmonella sp. in unfiltered Dworshak water, 3 August 1973

experienced a rapid reduction to 1.0×10^3 or 1.0×10^2 microorganisms/ml after 7 days, and after 14 days all species had declined to less than 9.0×10^1 microorganisms/ml. E. aerogenes and Salmonella maintained residual numbers, in the order of 10^1 cells/ml, for the duration of the experiment while E. coli and S. faecalis var. liquefaciens were completely eliminated.

When compared with the death rates in the filtered water membrane chambers, the microorganisms in the unfiltered water chambers decreased much more rapidly. For example, after the 14th day of the second membrane experiment all species in the filtered water membrane chambers were present at an average of 3.0×10^5 microorganisms/ml, while the species in the unfiltered water membrane chambers had declined to less than 9.0×10^1 microorganisms/ml. This observation is consistent with the findings of other researchers (14, 15), who have noted that bacteria survive longer in sterilized water than in natural water. It is, therefore, important that one is aware of the type of water being used as the supporting medium, for the relative death rates of microorganisms are definitely related to the water type being used. As noted by Heskins (16), the increased reduction of bacteria in unsterilized water was due to the presence of bacterial predators. Therefore, if bacterial survival experiments are conducted in water, the effects that these predators have on the bacterial death rates must be considered. The membrane chambers used in this study provide the means by which one can control the volume of the supporting medium, monitor the number of organisms present, and conduct a controlled field experiment that closely parallels natural conditions.

The relative death rates of the bacterial species were similar. These findings are in opposition to the observations of other researchers (17, 18) who found that S. faecalis var. liquefaciens and E. coli survived longer than Salmonella. When looking at Figs. 33, 34, and 35, it is obvious that the death rates of the microorganisms tested were not greatly different from one another. Such an observation adds support to the use of these microorganisms (E. coli, S. faecalis var. liquefaciens, and E. aerogenes) as indicators of fecal pollution, since their death rates resembled the death rate of a pathogenic microorganism (Salmonella).

Relationship of Total Bacteria, Soluble Carbon, and Total Coliforms to Other Parameters: Bacterial funtion in an aquatic system is primarily one of solubilization of immobilized nutrients, making those nutrients available for utilization by higher life forms and return of soluble nutrients to a usable state for utilization by other forms. In these processes oxygen is usually consumed and mineralized carbon is released. If sufficient quantities of organic substrate are available, O_2 levels will decrease and CO_2 content or the amount of carbon in the CO_2-HCO_3^--$CO_3^=$ equilibrium system will increase. The effect of bacterial activity in hard waters will usually be insignificant compared to the total mineral carbon in the system. In low alkalinity waters this effect could be detectable and significant. During the same functions, organic phosphorus, organic nitrogen, organic sulfur, and other essential mineral nutrients are released and again made available for use.

Some of these types of actions and reactions were typified by the correlations in Table 1. Correlations, where they existed in 1972, were primarily with organismic parameters such as total algae and zooplankton. In 1973 the correlations were mixed biological-chemical and in 1974 almost exclusively chemcal. The changes in correlated parameters are indicative of the changing conditions in the lake and the increasing complexity of interactions in the system. Consequently the stability of the system is increasing.

When values from all stations (surface) are used in the analysis, few correlations are high enough to be considered important. This lack is largely due to the distance separating the sampling points and the subsequent difference in water characteristics. However, when different sampling sites are evaluated separately, significant correlations are evident. At RM-3 surface in 1972 there was a high correlation between bacteria and total algae and also blue green algae. As shown in another part of this study, the bacteria-algae correlation is probably due to the growth of bacteria on algal biomass since almost 85% of the carbon fixed by algae is cycled through bacteria. This high level of bacterial carbon utilization is responsible for the correlations between bacteria and total algae and also blue green algae. This high level of bacterial carbon utilization is also responsible for the correlations between bacteria and soluble carbon, D.O., % saturation, HCO_3^-, and alkalinity. In the decomposition of algae biomass by bacteria, O_2 is utilized, CO_2 is produced and changes either the pH or the $CO_2 - HCO_3^- - CO_3^=$ equilibrium. In Dworshak where alkalinity is very low (5-20 ppm), effects of CO_2

production on alkalinity could be significant. This effect could be especially important if there was a shift in phosphorus levels to Vollenweider's (13) dangerous levels and massive primary production occurred.

Other correlations that occur between various parameters in the table are difficult to assess, and causes or relationships remain obscure. The many interactions and the complexity of the system is such that this is not surprising but is to be expected.

TABLE 1. SIMPLE CORRELATIONS ($F < 0.05$)

Site	X	Y-1972	r	Y-1973	r	Y-1974	r
All Stations, Surface	Total Bacteria	None	-	Soluble Carbon	-.25	None	-
	Soluble Carbon	Total Algae Blue-green Algae Zooplankton Total Organic Carbon	.44 .45 .43 .81	Bacteria Percent Saturation	-.25 -.23	None	-
	Coliforms	None	-	Secchi Disk	.24	None	-
RM-3, Surface	Bacteria	Total Algae Blue-green Algae Zooplankton Soluble Carbon HCO_3^-	.90 .91 .78 .71 -.64	Soluble Carbon Dissolved O_2 Total Alkalinity HCO_3^- Secchi	-.36 -.29 .48 .51 .37	None	-
	Soluble Carbon	Bacteria CO_2	.71 -.79	Bacteria NO_3	-.36 .57	None	-
	Coliforms	None	-	None	-	HCO_3^- NO_3 Percent Saturation CO_2	-.35 .65 -.43 .25

TABLE 1. (continued)

Site	X	Y-1972	r	Y-1973	r	Y-1974	r
RM-3, Deep	Bacteria	Green Algae	.81 .79	None	-	Dissolved O_2 Percent Saturation	-.40 -.39
	Soluble Carbon	None	-	Umhos	.49	Total Alkalinity HCO_3^-	.66 .66
	Coliforms	None	-	None	-	Temperature Umhos	.53 .48
RM-19, Surface	Bacteria	None	-	None	-	CO_2	.83
	Soluble Carbon	None	-	Total Algae Umhos	.69 .73	SO_4 Total Alkalinity HCO_3^-	.70 .72 .72
	Coliforms	None	-	None	-	Total PO_4 CO_2	-.63 .65
RM-19, Deep	Bacteria	NO_3	-.97	Total Algae HCO_3^- D. atoms Total Alkalinity Turbidity	.73 .73 .69 -.73 .71	None	-
	Soluble Carbon	None	-	None	-	None	-
	Coliforms	None	-	Blue-green Algae Si Secchi	.99 -.73 .79	PO_4^- Si	-.90 -.87

TABLE 1. (continued)

Site	X	Y-1972	r	Y-1973	r	Y-1974	r
RM-35, Surface	Bacteria	None	-	Dissolved O_2 Umhos	-.60 -.95	Umhos	.65
	Soluble Carbon	None	-	None	-	Total Alkalinity HCO_3^- Umhos	.79 .79 .72
	Coliforms	None	-	Green Algae Total Organic Carbon NO_3	.93 .73 -.61	SO_4	.59
RM-35, Deep	Bacteria	None	-	None	-	PO_4	.92
	Soluble Carbon	None	-	None	-	None	-
	Coliforms	None	-	SO_4 HCO_3^- Turbidity	.83 .69 .91	None	-
EC-4, Surface	Bacteria	None	-	Turbidity	.73	PO_4	.69
	Soluble Carbon	Total algae	.80	None	-	SO_4	.85
	Coliforms	Total Algae Umhos	.88 .88	HCO_3^- Total Alkalinity Diatoms	.52 .52 .71	SO_4 Percent Saturation Dissolved O_2 Umhos	.69 -.52 -.52 -.45

TABLE 1. (continued)

Site	X	Y-1972	r	Y-1973	r	Y-1974	r
EC-4, Deep	Bacteria	None	-	Total Algae Dictoms	.82 .71	PO_4	.63
	Soluble Carbon	None	-	None	-	None	-
	Coliforms	None	-	Total Organic Carbon	.93	None	-
LNFK-1, Surface	Bacteria	Si	.81	Dissolved O_2 CO_2	-.56 .75	Blue-green Algae Total Organic Carbon	.92
	Soluble Carbon	HCO_3^- Total Alkalinity	.82 .82	None	-	HCO_3 *Total Alkalinity*	.62 .62
	Coliforms	Diatoms	.96	None	-	None	-
LNFK-1, Deep	Bacteria	None	-	CO_2	.86	None	-
	Soluble Carbon	None	-	None	-	None	-
	Coliforms	None	-	None	-	None	-

CONCLUSIONS

1. Heterotrophic bacterial activity and heterotrophic bacteria numbers were high during summer months of the sample years.

2. High bacteria levels were due in part to recycling of primary production carbon.

3. Non-fecal coliforms were capable of growth in the reservoir and at times reached extremely high numbers. Since coliforms were not associated with a fecal source, the levels detected are not considered to be a violation of state standards, nor of public health significance.

4. Fecal coliforms were not present in the reservoir in significant numbers except at LNFK-1 during November 1973 when 45 fecal coliforms/100 ml were isolated from one sample.

5. Soluble carbon levels throughout the reservoir were decreasing and should stabilize at a fairly low level unless primary production increases, in which case high bacterial levels would occur and subsequently D.O. affect levels during summer stratification.

6. Primary production in the reservoir is phosphorus limited according to the algal assay procedure. According to the assay results and to supporting data, slight increases in phosphorus inputs would lead to greatly increased primary production levels.

7. Bacteria play a significant role in the cycling of nutrients in the system and may be significant in maintaining the alkalinity system.

8. Survival of indicator organisms under simulated reservoir conditions was quite long.

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